STUDIES ON PRECISION SEEDING, WATER DEFICITS AND OSMOTIC ADJUSTMENT OF GERMINATED SEED

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STUDIES ON PRECISION SEEDING, WATER

DEFICITS AND OSMOTIC ADJUSTMENT

OF GERMINATED SEED

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PREFACE

This study is concerned with technology developed to separate and precision meter germinated seed. The effects of water deficits on germination, early seedling growth and osmotic regulation is also explored.

Chapter III, Separation, Singulation and Precision Planting of Germinated Seed, was submitted to HortScience for publication. Chapter IV and V, Germination and Seedling Growth Characteristics of Three Tomato Species Affected by Water Deficits and Osmotic and Solute Regulation in Germinating Tomato Seedlings, were submitted to the Journal of the American Society of Horticultural Science for publication.

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CHAPTER I

INTRODUCTION

Sowing seed is an annual task in agriculture. It is of prime importance to obtain a good plant stand for maximum yield potential. Vegetable crops as well as agronomic crops require high quality seed for vigorous seedling emergence and subsequent plant growth.

There are two major methods for establishment of vegetable crops; transplanting and direct seeding. Transplanting is a costly operation and not practical with all vegetable crops. Transplant growing and planting is an energy and labor intensive operation. The production of transplants is costly and requires growing plants in a greenhouse, cold frame, hot bed or field bed and then setting the plants in the field. Feasibility of using transplants for establishing a particular crop is determined by: desired plant population, difficulty in seedling establishment by conventional seeding methods and the economic benefits obtained by earlier maturity of transplanted crops compared to direct seeded crops.

Direct seeding consists of sowing seed directly into the field. Poor environmental conditions for germination at time of seeding, soil crusting and soil pests can dramatically reduce the percent emergence. This common occurrence has resulted in over-seeding from two to ten times to insure an adequate plant stand. Over-seeding often requires thinning after plant establishment, a labor intensive operation.

Sowing germinated seed is an alternative for establishing vegetable crops. Seed are first germinated in aerated water till radicle emergence occurs. The germination process is better controlled as both water and oxygen are supplied. Temperature can be regulated to insure maximum uniformity and percent germination. The germinated seed is then suspended in a gel matrix and finally sown with appropriate planters. The term germinated seed will be used in this thesis and refers to a germinating seed in which the radicle is visibly emerged from the seed coat.

The germinated seed can be separated from the nongerminated and dead seed to achieve full potential of the seeding operation. Separation can be performed by exploiting density differences between seed with and without radicles visibly emerged (60). Desired solutions of specific gravity greater than water can be obtained by adding sucrose to water. Thus, a separation technique that results in a very high percentage of germinated seed combined with a planter that can singulate and precision place germinated seed would provide the ultimate in field seeding.

The advantages of sowing germinated seed or direct seeding compared with transplants are:

1. Lower establishment costs
2. Higher plant populations
3. Freedom of foliar diseases and nematodes due to infested transplants
4. Greater choice of cultivar
5. Faster planting rates

The advantages of sowing germinated seed compared with conventional seeding are:

1. Earlier emergence
2. More uniform emergence
3. Achieve better plant stand
4. Greater stress tolerance at time of planting

The advantages of transplants compared with direct seeding are:

1. Earlier maturity and marketing
2. Does not require thinning
3. More predictable plant stand

Poor environmental conditions at time of seeding and seedling establishment can be detrimental to the final plant stand. Environmental stresses include high or low soil temperature and excess or deficit soil moisture.

The germination process is very sensitive to adverse conditions. The following methods can help minimize the effects of environmental stresses on crop establishment:

1. Sow seed during a period of optimal environmental conditions for germination
2. Reduce the amount of time from seeding to seedling emergence
3. Overcome the germination steps (or process) that are most sensitive to environmental stress prior sowing
4. Plant species or cultivars that are better adapted to particular types of stress

It is often necessary to sow seed when field conditions are less than optimal due to a short growing season or the need to schedule crops for maximum production or marketing. Sowing a seed that is already germinated reduces the time to emergence. Thus the quicker the seedling is established the greater the chance of survival. In general, the germination process is more sensitive to environmental stresses than is seedling growth.

Crop establishment by seed in the semi-arid regions of the world is generally aggravated by water deficits. Drying winds can rapidly deplete the moisture from the top 2 to 3 cm of soil where most crop seed would be planted. However, ten cm below the soil surface adequate water exists for plant growth. High soil temperature often accompanies

water deficits. These elevated temperatures are often at or above the maximum cardinal temperature for germination of a given species.

Certain species possess adaptations that make their survival possible under adverse conditions. These adaptations are usually found in the established plant. It is of interest to determine if certain adaptations to particular environmental stresses also occur in the germination of that species.

It is necessary to understand the plant adjustment mechanisms in evaluating the germination and growth of seedlings under water stress. Plants can osmotically adjust (osmoregulation) to water deficits. The maintenance of turgor potential is necessary for growth to continue.

In conclusion, the concept of sowing germinated seed has many advantages over conventional seeding. The first studied is the density separation operation. Almost 100 percent germinated seed are obtained. The potential exists for obtaining a perfect field stand. The second is the establishment of seedlings in adverse environmental conditions. A germinated seed can continue to grow and develop in a stress which would normally be inhibitory to germination.

The objectives of this research were to:

1. Develop and refine a technique to separate germinated seed (seed with radicles visibly emerged) from non-germinated seed and utilize this technique in conjunction with a precision metering system developed by the O.S.U. Agricultural Engineering Department.
2. Evaluate the effects of water stress on germination and seedling growth of common tomato, Lycopersicon esculentum cv. Campbell 1327, and 2 wild tomatoes, Lycopersicon chilense and

and Solanum pennellii.

3. Measure the water relations of germinated tomato seed and quantify the osmotically active solutes accounting for the measured osmotic potential. To correlate growth of the hypocotyl and radicle with turgor potential.

CHAPTER II

LITERATURE REVIEW

Introduction

A method for sowing germinated seed in a fluid gel has been reported (17). The seed are first germinated in controlled conditions and then suspended in a fluid gel which is extruded behind the furrow opener of a conventional planter (22).

The major advantages of sowing germinated seed compared to dry seed are earlier and more uniform emergence (12). Another major advantage is the capability of a germinated seed to continue growth at sub-optimal environmental conditions for normal germination to occur. This point will be discussed later in further detail.

Techniques of Fluid Drilling

A method for germinating small quantities of seed has been described by Darby and Salter (15). A vertical transparent column is filled with water and aerated. Seed are suspended in the water by the air bubbles. There are provisions for changing the water to remove seed leachates that accumulate in the water during the germination process. Another system for germinating large quantities of seed has been developed (11). Seed are placed in nylon bags which are alternately steeped in clean water then placed in a spin drier to remove excess water and allow air movement to the seed. Seed germinated

using either technique are removed, when radicles are approximately 2 to 3 mm in length.

Several vegetable species germinate slowly and erratically even in ideal environmental conditions. The use of growth regulators is one method of overcoming the variability in germination. Sosa-Coronel and Motes (54) used gibberellic acid (GA_3) to increase the earliness and uniformity of germination in seven different types of pepper (Capsicum annuum). The optimum concentration of GA_3 was 200 to 400 ppm.

Further studies by Sosa-Coronel (53) determined that pepper seed germination in aerated columns can be accelerated using GA_3 at 6 ug/mg seed and 50 to 75 mg seed/cc of solution.

The following criteria were established to improve the percent germinated seed prior to fluid drilling:

1) separation process with a high efficiency,

2) rapid method for a large quantity of seed, and

3) non-destructive and non-phytotoxic to germinated seed.

The major advantages for performing a separation process are:

1) obtain nearly 100 percent germinated seed by eliminating the dead and slow to germinate seed and

2) reduce field skips in precision seeding and have the potential for 100 percent seedling emergence.

A method for separating germinated from ungerminated seed has been developed by Taylor et al. (60). The technique is based on density differences of seed with and without radicles. Seed with radicles are less dense than ungerminated seed. Specific gravity solutions for seed separation are obtained by using sucrose water solution.

The density separation removed 95 percent of the ungerminated seed for celery (Apium graveolens var dulce) and pepper. Over 95 percent

emergence was obtained by sowing the separated germinated seed for both crops (60).

A pre and post-radicle emergence separation method was later developed by Taylor and Motes (59). The float-sink principle in a sucrose solution was used as described earlier. Seed were germinated in aerated water and then separated into density lots when fully imbibed but prior to radicle emergence. This step reduced the inherent variability in the seed lot and also the variability due to differential seed swelling (volume change) during imbibition. The amount of water a seed imbibes and thus swells is determined by its chemical composition (40).

Each density lot continued germination until radicle length was optimal for fluid drilling. The post-radicle emergence separation resulted in 98.1 and 97.6 percent germinated seed for pepper and lettuce, respectively. The recovery of germinated seed was greater than 98 percent for both crops. The percent germination without separation was 80.6 and 86.3 percent for pepper and lettuce (Lactuca sativa), respectively. Thus the technique provides the potential for obtaining nearly 100 percent viable seed.

A once-over separation at time of radicle emergence was compared with the pre-post separation method. The percent germination was 96.1 and 95.4 and the percent recovery was 96.8 and 95.0 for pepper and lettuce, respectively. The pre and post-radicle emergence separation further improved the efficiency and the percent germinated seed.

Taylor et al. (61) have reported that the use of Maltrin $^{R}250$ is better suited for obtaining the desired specific gravity solution than sucrose. Maltrin $^{R}250$ is a water soluble, homopolymer of glucose. Sucrose solutions have been observed to be detrimental to germinated

seed due to the very negative osmotic potential. Maltrin ^{R}250, being a much larger molecule (ca. 80,000 m.w.) than sucrose, does not result in a large decrease in osmotic potential of the separating solution.

Storage of germinated seed is necessary if planting operations are delayed. Germinated seed of cool season crops have been stored for up to two weeks in an ice bath (0^{o}C) without detrimental effects on subsequent growth (11). Taylor (57) has shown that germinated pepper and tomato seed held at 5^{o}C for 6 days resulted in decreased emergence. The decline in seedling emergence was attributed to chilling injury.

Storage of germinated pepper seed at temperatures lower than 5^{o}C for longer than 2 days resulted in a decrease in the total and rate of emergence (53). Sensitivity of chilling injury was cultivar dependent with cv. California Wonder Select being the most sensitive tested.

The fluid gel matrix acts as a carrier to facilitate planting and prevents damage to the exposed radicles. The requirements for a gel are: that it suspend seed, be economical, easily prepared, non-corrosive to equipment, non-toxic to seed, insensitive to water quality and easily cleaned from equipment (42). Methods have been described by Sosa-Coronel et al. (55) to evaluate gels for phytotoxic properties to germinated seed.

Planters to sow germinated seed have been designed by workers at the National Vegetable Research Station (10, 38). A combination fluid drill and dry seed planter for vegetable plot research has been developed by Spinks et al. (56). The advantage of this planter is that both dry and germinated seed can be sown with the same planter for study comparisons.

Searcy (50) has developed a metering system which can singulate

and precision plant germinated seed. Further studies to evaluate the metering system were described by Taylor et al. (61).

Results From Fluid Drilling

Results showing earlier and more uniform emergence and increased yields by sowing germinated seed have been reported by several workers (43, 44, 58). These results have largely occured when seed were sown at suboptimal environmental conditions for germination to occur.

The minimum cardinal temperature for tomato seed germination is approximately 10-12°C (5). If the seed was first germinated in ideal conditions and then sown at low temperatures (10-12°C) growth will continue (5). Price, et al. (47) has shown the time to 50 percent emergence for tomato at 12.5°C was reduced from 28.8 days for dry seed compared to 6.6 days for germinated seed.

Certain varieties of lettuce and celery germinate poorly, especially in darkness. Germination in light containing red frequencies overcomes this dormancy and then these seed can be sown in the field (9).

Thermal dormancy occurs in certain cultivars of lettuce (23). Lettuce seed will germinate poorly in soil temperatures above 25°C. If lettuce seed are first germinated in ideal conditions at optimal temperatures then they may be sown at elevated soil temperatures and growth will continue.

Wild Species of Tomato

Interspecific hybridization is playing an increasingly important role in the breeding of improved cultivars of higher plants. Tomato (Lycopersicon esculentum) has been improved in this fashion. One major

accomplishment in tomato varieties has been the incorporation of disease resistance.

A number of wild species of tomato has been described by Rick (48). These relatives of cultivated tomato have been found to contain many desirable traits. The following is a list of species and their particular trait of interest:

Genus Species	Trait
1. L. esculentum var. cerasiforme	high moisture tolerance and disease resistance
2. L. minutum	high sugar content of fruit (10-11% soluble solids)
3. L. peruvianum	salt tolerance
4. L. cheesanii	salt tolerance
5. L. hirsutum	insect resistance
6. Solanum pennellii	drought and salt tolerance
7. L. chilense	drought avoidance

Solanum pennellii and L. chilense are of interest in this study for their drought resistant characteristics. S. pennellii is found on the west slopes of the Andes in central Peru. It has been found in the more arid regions of its habitat growing with only cacti and bromeliads (48).

The root system of S. pennellii amounts to less than 5 percent of the proportional weight of L. esculentum. The leaves of the wild species resist drought by evolving a high capacity to absorb and retain atmospheric moisture. Dehan and Tal (16) have shown that S. pennellii is salt tolerant as well as drought tolerant. Lycopersicon chilense, unlike S. pennellii, has a very extensive root system and therefore can be classed as a drought avoider. The leaves of L. chilense do not retain water as do S. pennellii's. L. chilense is self-incompatible requiring

either insect or hand pollination. S. pennellii in contrast is self-pollinated and self-fruitful.

Seed Germination and Water Stress

The germination of planted seed and subsequent development of crop plants is of great importance in agriculture. Germination, emergence and early seedling development are critical stages in plant development as they affect density of the plant stand, degree of weed infestation and also limit yield.

Germination problems are more extensive under semi-arid and arid conditions. Under these conditions the rate of soil moisture evaporation is high, soil crusting can occur and soil salinity problems may result. High soil temperatures generally accompany dry soils. Though soil moisture may be adequate for plant growth, often the surface layer of soil dries too rapidly and prevents seed germination and seedling establishment.

The physiology of seed germination has been reviewed by Mayer and Poljakoff-Mayber (40). This topic will not be summarized in this thesis.

The effect of soil moisture on seed germination has been reviewed by Hillel (31). In his review Hillel established 6 areas that relate to the physiological behavior and basic environmental requirements for germination of a particular species. These characteristics are:

1. The sorption isotherm, or "seed moisture characteristic": the relationship of the seed's water content to its water potential.
2. The critical potential, or "threshold potential": the lowest value of water potential at which the seed can germinate.
3. The possible presence of germination inhibitors, and the mode and rate of their dissipation.
4. The time rate of imbibition, the time required for germination

(radicle emergence), and time rate of rootlet elongation at different ambient temperatures and water potential values.

5. Critical hydration levels of the seed: the minimal water content at which the seed begins to germinate, and the hydration level at which seed water uptake becomes biologically irreversible.

6. Critical depth of emergence: the maximal depth from which the seedling, once germinated, can successfully emerge.

This thesis will be involved with points 2 and 4 from the above discussion. That is, the effects of water stress on the physiology of seed germination and on germinated seed.

It has been shown by Hegarty and Ross (26) that in calabrese (Brassica oleracea var italica) and cress (Lepidium sativum) that radicle growth immediately after germination was less sensitive to water stress than during germination. A later study by Ross and Hegarty (49) reported that a similar response to water stress was found in 7 different families of vegetables consisting of 13 species.

Obroucheva (45) has found that the initiation of cell elongation and cell elongation itself in roots are under different metabolic control. Hegarty (25) has suggested that the initiation of cell elongation may be the process in seed germination that is most sensitive to environmental stresses.

Hegarty and Ross (27) reported that seed of calabrese were 'primed' by placing the seed in a -10 bar solution of polyethylene glycol (PEG 6000) for 10 days. This treatment prevented radicle emergence but brought the seed to the 'brink of germination.' The seed were then transferred to pure water for various lengths of time. Four hours after the seed was transferred to water the moisture content of the seed increased and 53 percent of the seed germinated. Seed transferred to

water for 16 hours resulted in 96 percent germination. Those germinated seed were transferred back to the -10 bar PEG solution and they were able to continue growth after the water stress was reimposed.

This experiment suggested that the water stress sensitive stage occurred very shortly before growth (radicle emergence) started. The second conclusion was that seed with radicles emerged can continue growth in a water stress that was totally inhibitory to their germination. The initiation of cell elongation was associated with osmotic adjustment. This point will be discussed in a later section.

The effects of water stress have been associated with alterations in the levels of endogenous growth regulators (4). Hegarty and Ross (28) have shown that growth regulators can remove the differential sensitivity to moisture stress during seed germination and seedling growth of red clover (Trifolium pratense). A combination of 2.0 mM ethephon and 0.3 mM kinetin removed the differential sensitivity to moisture stress. Though germination was normal subsequent growth of the seedlings was inhibited. This implies independent control of germination and growth. In a similar experiment performed with calabrese seed, no combination of gibberellic acid, kinetin and ethephon would completely remove the differential sensitivity to moisture stress.

Seed Germination and High Temperature Stress

Temperature effects on germination can be expressed in terms of cardinal temperatures: minimum, optimum and maximum (7). The maximum cardinal temperature for tomato germination is approximately 35°C (39). Berry (3) has shown varietal differences in tomato germination at high temperatures. The cultivar Campbell 1327 was found to have 3 to 6

percent germination at 35°C depending on seed source.

High temperature stress effects on plants has been reviewed by Levitt (37). Little work has been undertaken on the upper temperature limits of seed germination. Much of the existing information on seed germination at high temperatures has been from studies on lettuce. Light requirement interacts with thermodormancy in lettuce. Thus the mechanism of lettuce seed germination at high temperatures may be different from other species.

A study by Hendricks and Taylorson (30) has shown a leakage of amino acids occurs when seed of certain species are imbibed at 30-35°C. This was explained by a change in membrane permeability at the high temperatures.

Plant Responses to Water Stress and Osmoregulation

Life evolved in the medium of water. Plants are dependent on water for function and survival. Water plays many roles in plants including; a reactant in biochemical reactions serving as a medium for the ionization of metabolites, photolysis of water in photosynthesis and being the inflating agent in maintaining structure and rigidity.

The topic of plant responses to water stress has been reviewed by Hsiao (33). In his review he summarized the generalized sensitivity of plant processes to water stress (Table 1).

Cell growth is the most sensitive process to water stress. Cell growth consists of cell division and elongation. A loss of water from plant tissue has the following direct effects as summarized by Hsiao, et al. (34):

TABLE I

GENERALIZED SENSITIVITY TO WATER STRESS OF PLANT PROCESSES OR PARAMETERS[a]

Process or Parameter Affected	Sensitivity to Stress: Very Sensitive → Relatively Insensitive; Reduction in Tissue ψ Required To Affect Process[b]: 0 bars, 10 bars, 20 bars	Remarks
Cell growth		
Wall synthesis		Fast growing tissue
Protein synthesis		Fast growing tissue
Protochlorophyll formation		
Nitrate reductase level		
ABA accumulation		
Cytokinin level		
Stomatal opening		Depends on species
CO_2 assimilation		Depends on species
Respiration		
Proline accumulation		
Sugar accumulation		

[a]Length of the horizontal lines represents the range of stress levels within which a process becomes first affected. Dashed lines signify deductions based on more tenuous data.

[b]With ψ of well-watered plants under mild evaporative demands as the reference point.

1. reduction in the chemical potential of water,
2. concentration of macromolecules and of solutes of low molecular weights,
3. changes in spatial relations in membranes and organelles through the reduction in volume and
4. reduction of hydrostatic pressure (ψp) inside the cells.

A reduction in the chemical potential would only be 0.4 and 0.7% if ψ was reduced by 5 and 10 bars, respectively. Thus this would be insignificant. The concentration of solutes would only be a problem if certain allosteric enzymes were involved. These enzymes would have to be extremely sensitive to small changes in the concentrations of molecules. Due to the nonstatic nature of membranes, little effect would be caused. A reduction of turgor (ψp) has been shown to directly affect crucial physiological processes.

Water movement in a plant is passive and moves down a free energy gradient. Classical water relations can be expressed in the following equation:

$$\psi = \psi p + \psi s + \psi m$$

ψ is the water potential and is the amount of free energy available to do work. The potential of pure water has a value of 0. ψp is the pressure potential. It is a positive value and is derived from the hydrostatic pressure that developes within a cell. ψs is the osmotic potential. It is determined by the colligative properties of molecules dissolved in pure water. ψm is the matric or suction potential. Water relations are frequently expressed in bars.

The maintenance of a positive pressure potential is essential for growth to continue under water stress. Growth will continue till ψp decreases to a critical threshold potential (33). Kirkham et al. (36) and others (33) have reported on the role of turgor on cell enlargement

and division.

Osmoregulation or osmotic adjustment is a process in which turgor is maintained while the water potential decreases (33). This occurs due to a decrease in the ψ_s and ψ_m.

Wiebe (62) has found that the matric potential was negligible until tissue was badly dehydrated. During water stress an increase in solute content (ψ_s) per cell occurs, either by exogenous uptake or by internal production of osmotically active substances.

The topic of osmoregulation has been reviewed by Hellebust (29). The major osmotic components of glycophytes are potassium salts of organic acids and sugars. Malate was the organic anion most frequently involved in the balancing of excess cation uptake. In halophytes, sodium and chloride usually account for the major portion of total osmotic solutes. Proline and betaine (glycine) have also been observed to accumulate under water and salt stress in certain species (29).

The physics of turgor and osmoregulation has been reviewed by Zimmermann (63). Wall-less cells respond to a decrease in water potential by decreasing their cell volume. Walled cells, on the other hand, undergo little change in volume in response to water stress. They respond by changes in turgor potential.

A biphasic osmotic regulatory response to water stress has been described (63). When a cell was placed in a hypertonic solution it lost its turgor in minutes. After a period of time, generally hours or even days, a cell regains its turgor almost to the same magnitude that was observed before the stress was applied.

Much of our understanding of osmoregulation comes from the study of marine algal cells (32). The algae most frequently studied are large,

simple cells which make measurements of pressure potential relatively simple. The mechanism for turgor-triggered processes appear to be under direct control of membrane transport and the electrical properties of the cell membrane (63).

Osmoregulation by Internal Production of Substances

Plants can generate their own osmotically active substances through metabolic pathways. Another method of osmotic adjustment is by retranslocation of existing solutes or ions within the plant.

Germinating seed or very young seedlings appear to have a great capacity for osmotic adjustment when water is limiting. Roots of 3 to 5 day-old pea (Pisum sativum) seedlings were shown by Greacean and Oh (24) to adjust their osmotic potential when grown in soil ranging in ψ from -2.8 to -8.3 bars. Root pressure potential was maintained and growth unaffected by decreasing soil and water potential.

Meyer and Boyer (42) have measured ψ and ψs of intact hypocotyls of soybean (Glyine max) seedlings at various water stresses. Withholding water from the hypocotyls resulted in osmotic adjustment of the hypocotyls so that turgor remained almost constant. Turgor was maintained until growth completely stopped. The cotyledons were the source of solutes for osmotic adjustment since removal of cotyledons prevented osmoregulation to occur.

Work by McNeil (41) has shown that osmotic regulation occurs in seedling sunflower (Helianthus annuus) hypocotyls. The mechanism appears to be similar to soybean that was previously described by Meyer and Boyer(42). The principal osmotic substances present were hexoses (glucose and fructose) and organic potassium salts. Potassium salts and

carbohydrates were not available in the growing medium. Thus internal osmotic pressures and hence turgor were maintained by (1) translocation of sucrose from the cotyledons and later inversion in the hypocotyls and (2) translocation of potassium from the seed to the hypocotyls.

Sharp and Davies (51) have performed experiments with corn (Zea mays) seedlings grown in pots and subjected to a water stress. Leaf extension was completely arrested by withholding water from the plants for several days. Root growth during the same period was unaffected by the water stress. The authors found that the root pressure potential was maintained by a decrease in the osmotic potential. It was assumed that a net accumulation of solutes occurred, but the solutes were not identified or quantified in the study. An increase in the root to shoot ratio was observed with increasing water stress. The data suggests that solutes were partitioned to the roots so that turgor and hence root growth were maintained during mild water stress.

Hsiao (33) has concluded that osmotic adjustments to water stress probably occur slowly and to only a limited extent in shoots of many species. Osmoregulation in roots does occur, as already cited, and may be part of the reason for the increase in root to shoot ratio during stress in dry soils (18, 51).

The internal water relations of cotton leaves were determined for plants grown under water stressed conditions (13). Leaves of stressed plants maintained turgor; however, analysis of soluble sugars and malate could not account for the turgor potential. The authors concluded that structural changes occurring during stress may play a role in turgor maintenance.

Osmotic adjustment in sorghum leaves in response to water deficits

has been described by Jones and Turner (35). Plants were subjected to slowly drying soil to simulate field conditions. Water relations and relative water content of leaves were determined over time. Osmotic potential of leaves decreased as water stress increased. The volumetric elastic molulus (ε) was calculated from the ratio of the turgor potential to relative water content. As water deficits developed an increase in the ε or a decrease in the tissue elasticity occurred.

Studies of Gardener and Ehlig (21) and Dainty (14) have shown that the ε is strongly dependent on the turgor potential and cell volume. Thus the maintenance of turgor depends on both osmotic adjustment and cell elasticity.

Data thus far have shown osmotic adjustment to occur in hours to several days. Acevedo et al. (1) have shown that osmotic adjustment occurred in maize and sorghum (Sorghum bicolor) in the field and exhibited diurnal trends. Further studies (20) have shown that seasonal osmotic adjustment occurred in field grown sorghum and maize in response to moderate water stress.

Osmoregulation by Exogenous Solutes

A number of lower aquatic plants and higher plants have shown osmotic adjustment if the external medium contains absorbable solutes (8). Osmotic adjustment appeared to occur slowly and to a limited extent when Avena coleoptiles were placed in a -10 bar solution of mannitol (46). Osmotic adjustment occurred rapidly when exogenous sucrose was supplied. Sucrose in the medium also resulted in increased coleoptile elongation rates.

Sucrose has been found to be the best carbon source for growth of

excised tomato roots (6). Glucose grown roots contained sucrose synthetase and sucrose phosphate synthetase activity. However, glucose grown roots were found to contain less sucrose than sucrose grown roots. This indicates that the enzymes are not sufficient to support the synthesis of sucrose to levels which permit maximum root growth. It has been suggested that sucrose was involved with critical morphogenetic roles not carried out by glucose (6).

McNeil (41) has suggested the following pathway for accumulation of hexoses from sucrose in sunflower seedlings:

1. Transport of sucrose from the cotyledons via the phloem.
2. Sucrose is unloaded from the phloem to the symplast.
3. Transport of the sucrose into the vacuole down a sucrose concentration gradient. The gradient is maintained by hydrolysis of sucrose to glucose and fructose.
4. Low hexose efflux from the vacuole, thus preventing loss from the vacuole.

Slatyer (52) has shown the effect of various osmotic substances on the water relationships of tomato. Tomato plants at the 5th true leaf stage were transferred to culture solutions containing -5 and -10 bar concentrations of KNO_3, NaCl, sucrose and mannitol. All plants initially wilted, but quickly regained turgor after 28 hours except for the mannitol treatments. Full recovery of water content and turgor was associated with a decrease in osmotic potential. $Na^{36}Cl$ illustrated a close relationship between osmotic adjustment and ion uptake.

Erlandsson (19) has shown that both water and K^+ ion uptake immediately decreased when wheat (Triticum aestivum) plants were transferred from one nutrient solution to another nutrient solution containing

-5 bar PEG. The author suggested that the rapid change in water potential of the plants had effected the active ion transport mechanism.

Bernstein (2) has found osmotic adjustment to occur in pepper and bean (Phaseolus vulgaris) as the salinity of the medium increased. This adjustment took at least 24 hours under mild salinity stress to several days under a greater stress.

The differences in uptake observed from Erlandsson's and Bernstein's studies may be related to the time of sampling. Erlandsson measured uptake within 160 minutes after transfer to the water stress. The plants were experiencing a rapid decrease in turgor and ion uptake. Bernstein sampled every 12 hours. Thus sufficient time was allowed for osmotic adjustment to occur.

Cram (8) has reported that KCl is accumulated to a fairly constant internal concentration independent of the external concentration. Consequently, as turgor decreased there was not an increase in the influx of KCl. A similar mechanism has been reported for KNO_3.

In conclusion, osmotic adjustment has been observed to occur in a number of plant species, in different plant parts and at different stages of plant development. Osmoregulation can occur either by internal production of osmotically active substances, retranslocation of existing substances and by the uptake of exogenous solutes from the growing medium.

CHAPTER III

SEPARATION, SINGULATION AND PRECISION PLANTING OF GERMINATED SEED[1]

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Abstract: Cabbage seed germinated in aerated water went through a pre and post-radicle emergence separation by specific gravity to separate germinated from non-germinated seed. The desired specific gravity solutions were made with Maltrin ^{R}250 and water. The percent germinated seed after separation and the recovery of germinated seed was 99.3 and 95.1, respectively. A metering system was developed to precision plant the germinated seed. Metering rates of 0.5 and 2.0 seed/sec. were tested in the lab and greenhouse. Laboratory tests resulted in 5.7% doubles and 4.9% skips at 2.0 seed/sec. Greenhouse seedling emergence test resulted in 8% doubles and 15.6% skips at the fast rate. Spacing uniformity was acceptable for all tests.

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Crop establishment is an age old problem in vegetable production. Several strategies have been developed to insure a proper plant stand. Transplanting is a costly operation and practical only with some vegetables. Direct seeding requires thinning, a labor intensive operation. Other methods, such as seed tapes and pelletized seed, have been developed to achieve precision in planting but these methods do not insure germination and seedling emergence. To plant a crop directly and assure a field stand requires both accurate metering and a very high percentage of seedling emergence.

The concept of sowing germinated seed is a partial alternative to solving the problem of seedling emergence. The methodology of planting germinated seed has been described by Currah et al. (2). The system of fluid drilling consists of germinating seed in aerated water until radicle emergence, mixing the seed in a gel, and sowing with an appropriate drill. Taylor (4) and Biddington et al. (1) have reported that sowing germinated seed increased the earliness and uniformity of emergence as compared to conventional seeding methods.

A method to separate germinated from nongerminated seed by specific gravity has been described by Taylor et al. (5). The technique consisted of separating germinated (seed with visible radicles) from nongerminated (seed without radicles) seed by density differences in a sucrose water solution. The process removed over 95% of the nongerminated seed for celery and pepper. Planting the separated (germinated fraction) seed increased the percent and rate of emergence compared with germinated but nonseparated seed.

A pre-radicle and post-radicle emergence separation process has been described by Taylor and Motes (6). Germinating seed are separated

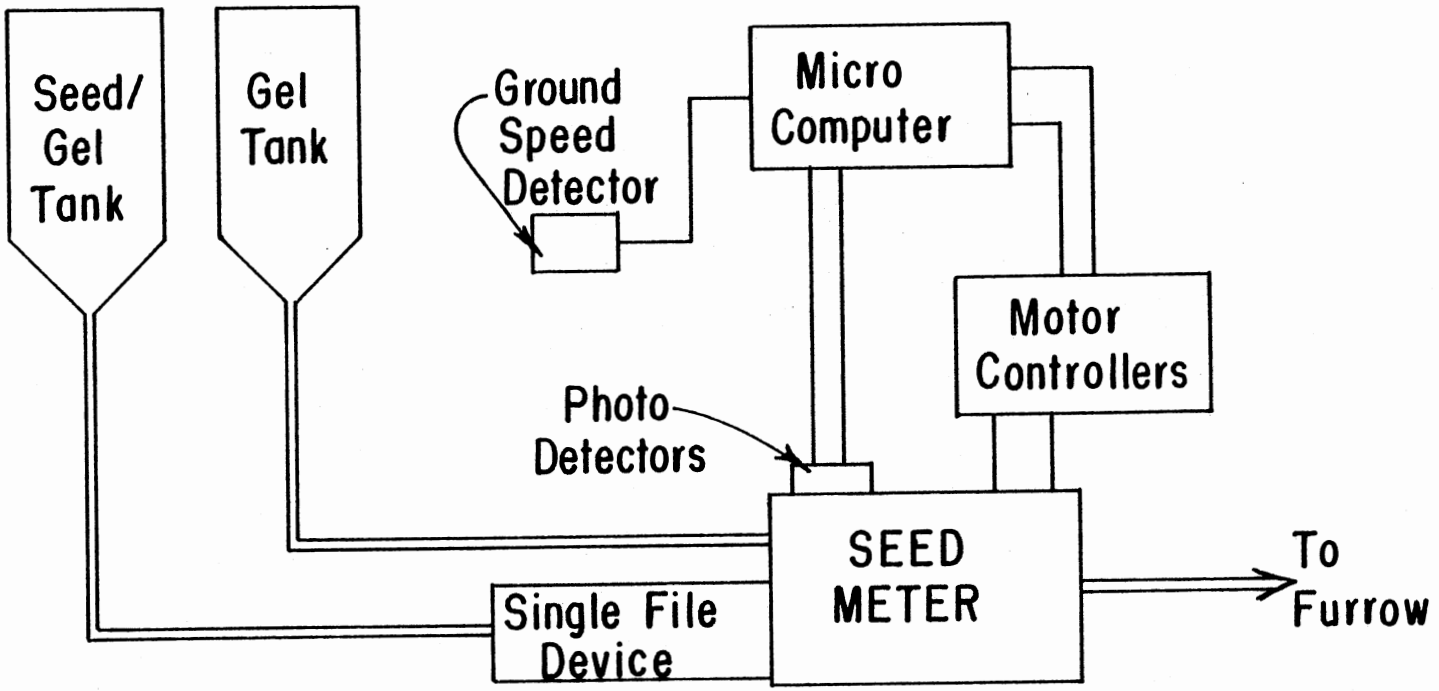
into density lots prior to radicle emergence. Each lot continues germination in aerated water, until radicle emergence is optimal for fluid drilling. A second separation is performed to separated germinated from nongerminated seed. This technique has resulted in 98.1 and 97.6% germinated seed for pepper and lettuce, respectively.

The second requirement for planting to stand is the ability to accurately meter and plant the seed in the desired location. Searcy (3) developed a metering system which could handle the fragile germinated seed. The system was microcomputer controlled and utilized photoelectric detectors to sense the seed to be metered. Seeds were suspended in a gel and moved through the metering mechanism by pressurizing the holding tank. Figure 1 shows a schematic of the metering system. The microcomputer detected ground speed and seed presence and operated the metering mechanism based on the conditions of those inputs. The system was evaluated on a laboratory test stand using a continuous belt to simulate planter travel. The metering system was capable of uniformly metering germinated cabbage seed without damage to the seed.

Seed Separation

Cabbage (Brassica oleracea var capitata L. cv Golden Acre) was evaluated for separation and precision metering experiments. Four replications of 1,000 seed were germinated in glass columns, 40 x 4 cm filled with distilled water at 25°C and aerated by an airstone at the base of each column. Seed were aerated for 8 hours and then removed from the aeration column for the pre-radicle emergence separation. The apparatus for seed separation consisted of a vertical glass column 30 x 7 cm fused to a funnel at the base of the glass column, fitted

Figure 1. A Schematic of the Metering System for Pregerminated Seed.


Seed/
Gel
Tank
Gel
Tank
Ground
Speed
Detector
Micro
Computer
Motor
Controllers
Photo
Detectors
SEED
METER
To
Furrow
Single File
Device

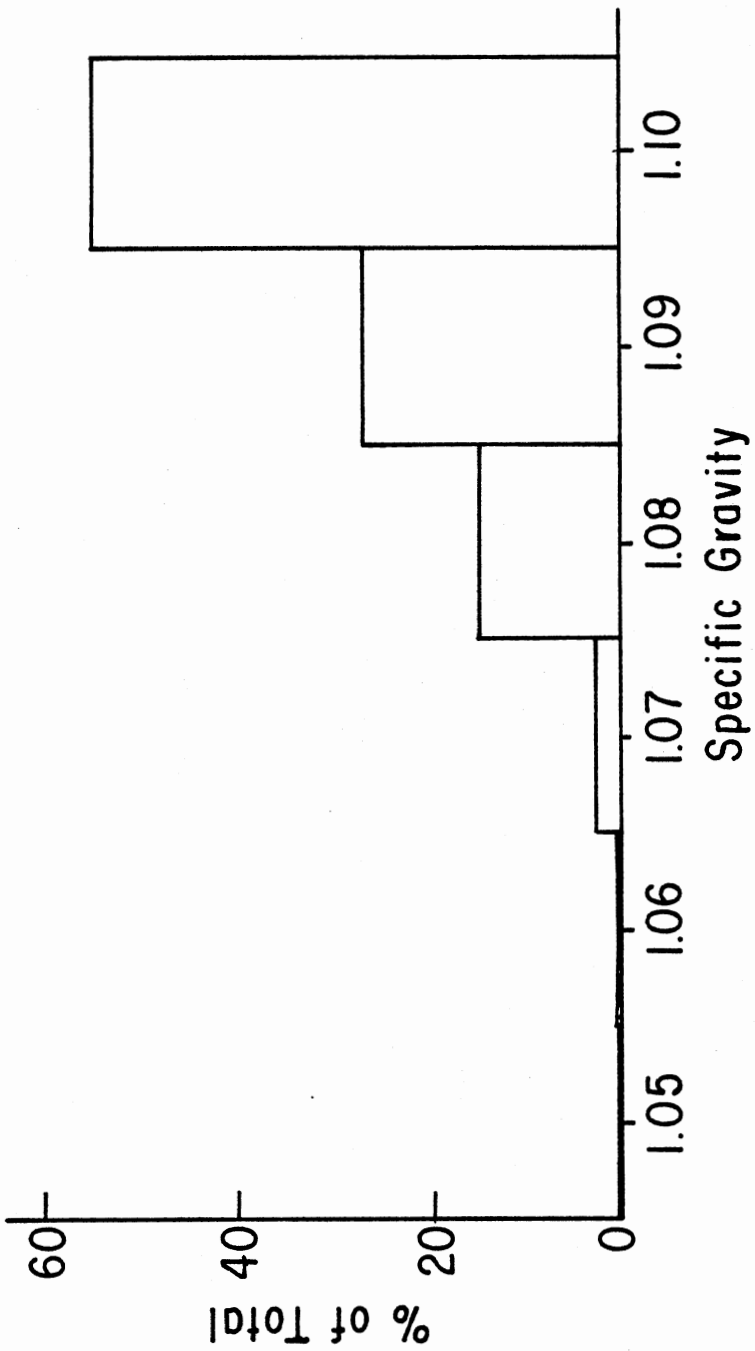
with tygon tubing and clamp (5). Seed were consecutively placed in solutions of known specific gravity from high to low density with 0.01 gradation.

Maltrin ^{R}250 (Grain Processing Corp., Muscatine, Iowa) was used instead of sucrose to obtain the desired specific gravity. Maltrin ^{R}250 is a water soluble homopolymer of glucose. Seed exposed for 5 minutes to a sucrose water solution of appropriate specific gravity resulted in abnormal growth of seedlings and browning of the exposed radicle. No visible distortion of growth was noted for a similar exposure to Maltrin ^{R}250 water solution (data not shown).

Seed that sank at a known specific gravity were recovered and placed back in aeration; those that floated were removed and placed in the next less dense solution. From this seed lots corresponding to densities equal to or greater than 1.10, 1.09, 1.08 g/ml were obtained. Seed of 1.07 g/ml or lower (3.7% of total) were discarded. This operation continued until all seed sank. Seed of each density were aerated for an additional 16 hours until radicles were approximately 2 mm in length. A second (post-radicle emergence) separation was performed on each density group to separate germinated from nongerminated seed. Seeds were considered germinated if the radicles were visibly emerged. The percent germinated seed and the percent recovery of germinated seed was calculated for each density lot.

The density distribution of imbibed seed is illustrated (Figure 2). Separating seed prior to radicle emergence reduced the variability in the density of the germinating seed lot. The density variation is due to inherent variability in the seed lot and seed composition which determines the amount of water the seed imbibes.

Figure 2. Pre-radicle Emergence Density Distribution of Cabbage cv Golden Acre.


% of Total
60
40
20
0
1.05
1.06
1.07
1.08
1.09
1.10
Specific Gravity

Post-radicle emergence separation resulted in a weighted total of 99.3 germinated seed and 95% recovery of germinated seed compared to 85.2% germinated seed without separation (Table 1). The weighted total was determined by the number of seed in each fraction and the percent germinated seed after separation in that fraction. The percentage of the total number of germinated seed that were in the floating fraction was termed the recovery.

Precision Planting

Preliminary testing was performed with cabbage in the laboratory. The precision metering system was further evaluated under simulated field conditions by sowing the separated germinated seed in the field soil of a greenhouse.

A Planet Jr. shoe and presswheel assembly was used with the system to place the metered seed into the soil. The seed were mixed into a 1.0 percent (by weight) solution of Viterra II Gel (Nepera Co., Harriman, NY) at the rate of 2 ml/seed. The seed were mixed into the gel by hand to achieve the most uniform distribution of seed.

The seed/gel mixture was placed in a holding tank and pressurized with compressed air. This pressurization procedure provided a constant pressure/variable flow of the mixture into the metering mechanism. Prior to moving into the metering mechanism, the seed passed through a single file device. The funnel shaped device, with an outlet slightly larger than the seed diameter, caused the seed to pass the first photoelectric detector one at a time and allowed the seed to be singulated by the metering mechanism.

The output of the metering system was dependent on two variables;

Table 1. The percent and recovery of germinated seed (± SE) of Cabbage cv Golden Acre after post-radicle emergence separation.

Seed Density Fraction (g/ml)	Percent (± SE)	
	Germinated Seed After Post-Radicle Separation	Recovery of Germinated Seed
1.10	99.4 (±.03)	95.6 (±.19)
1.09	99.3 (±.07)	94.9 (±.23)
1.08	98.9 (±.11)	93.2 (±.06)
Weighted Total	99.3 (+.02)	95.1 (+.06)

Percent Germination Without Separation was 85.2 (±.25)

the desired plant spacing, and the travel speed. The metering rate could be changed by varying either of the variables. In order to conserve limited greenhouse space, a spacing of 50 mm was chosen. The planter travel speed was varied in order to achieve metering rates of 0.5 and 2 seed/sec. These rates were chosen on the basis of previously conducted laboratory tests. There were four replications at each metering rate.

After emergence, the spacings between seedlings were measured and the data analyzed to determine the number of metering errors and the spacing uniformity of the correctly metered seedlings. Any spacing less than 50 percent of the desired spacing (25 mm) was considered a double, and spacings greater than 150 percent (75 mm) were considered skips. Each double or skip was considered a metering error. For purposes of determining uniformity of spacing, only the correctly metered seeds were considered.

Table 2 contains data on metering error and spacing uniformity for each metering rate for laboratory and greenhouse studies. At both metering rates the percent of total error was high. The greatest error in the greenhouse came in the form of skips. This is directly opposite to the results from laboratory studies. The skips could have resulted from seedlings not emerging from the soil. The large number of skips in the greenhouse was probably due to the difficulty encountered in maintaining a uniform depth of planting. The percent error was similar for both metering rates in both cases, higher than the error measured in the laboratory. This trend was expected due to problems with ambient light affecting the photoelectric detectors.

The uniformity of the spacing was generally acceptable at both

Table 2. Metering error and spacing uniformity for 0.5 and 2.0 seed/sec. in laboratory and greenhouse tests.

Metering Rate Seed/Sec.	Test	Metering Error			Spacing Uniformity		
		Percent Doubles	Percent Skips	Percent Total Error	Mean (mm) Spacing	Standard Deviation	Coeff. of Variation
0.5	Laboratory[z]	8.4	6.7	15.1	111.3[y]	7.30	6.6
	Greenhouse	9.2	14.9	24.1	47.8	5.54	11.6
2.0	Laboratory[z]	5.7	4.9	10.6	112.6[y]	19.10	17.0
	Greenhouse	8.0	15.6	23.6	49.2	7.38	15.1

[z]Emergence not a factor.

[y]Target spacing was 120 mm.

metering rates. The amount of variation in spacing that would be acceptable would depend on the crop being planted. As expected, the coefficient of variation increased with increase metering rate, although not as sharply as in the laboratory tests.

Conclusions

The separation technique is rapid, inexpensive and can be used to separate large quantities of germinated seed. The use of Maltrin $^{R}250$ is better suited than sucrose to obtain a desired specific gravity solution due to the very negative osmotic potential that is generated in the sucrose-water solution.

The precision planting metering system, as designed, operated slowly and with more errors than acceptable for a precision planter. However, the system shows promise for use in planting crops directly to stand. With appropriate redesign, the mechanism could be made to operate with greater accuracy at acceptable metering rates.

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CHAPTER IV

GERMINATION AND SEEDLING GROWTH CHARACTERISTICS OF THREE TOMATO SPECIES AFFECTED BY WATER DEFICITS[1]

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Abstract: Seed of Lycopersicon chilense, L. esculentum 'Campbell 1327' and Solanum pennellii were used to evaluate the effects of water deficits on germination and early germinated seed growth at 25, 30 and 35°C. Water stresses were maintained by solutions of polyethylene glycol (PEG) 6000 as an osmoticum of 0 to -8 bars in 2 bar increments. Germination of dry seed was more sensitive to water stress than germinated seedling growth of each species. Germination and seedling growth of L. chilense and S. pennellii were more sensitive to water stress than L. esculentum at 25°C. Germinated seed of all species were able to continue growth at

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35°C plus water stress while germination under the same conditions was totally inhibited. In general, the seedling root to shoot length ratio increased as water stress increased. The water sensitive phase of germination occurs just prior to visible radicle emergence. Emergence parameters were not affected by sowing germinated seed in a simulated drying soil condition. Sowing dry seed under the same conditions resulted in a decrease in the percent emergence.

Introduction

A method for sowing germinated seed in a fluid gel has been reported (5). The seed are first germinated in controlled conditions and then suspended in a fluid gel which is extruded behind the furrow opener of a conventional planter.

The major advantages of sowing germinated seed compared to dry seed are earlier and more uniform emergence (3). Another major advantage is the capability of a germinated seed to continue growth at suboptimal environmental conditions for normal germination to occur.

Thermal dormancy and light requirements for germination occurs in certain cultivars of lettuce. If lettuce seed are first germinated in ideal conditions at optimal temperatures and in light containing red frequencies, the seed will continue growth at elevated soil temperatures (7).

The minimum cardinal temperature for tomato seed germination is approximately 10-12°C (2). Growth will continue if tomato seed are first germinated in ideal conditions and then sown at low temperatures (2). It has been reported that the time to 50 percent emergence for tomato was reduced from 28.8 days for dry seed compared to 6.6 days for germinated

seed at 12.5°C (17).

Germination and seedling emergence problems are extensive under semi-arid and arid conditions. Under these conditions the rate of soil moisture evaporation is high, soil crusting can occur and soil salinity problems may result. High soil temperatures generally accompany dry soils. Though soil moisture may be adequate for plant growth, often the surface layer of soil dries too rapidly and prevents seed germination and seedling establishment. Sowing germinated seed is a possibility for assuring an adequate plant stand under such conditions.

It has been shown in calabrese (Brassica oleracea var italica Plenck.) and cress (Lepidium sativum L.) that continued radicle growth was less sensitive to water deficits than germination (10). A similar response to water stress was observed in 7 different families of vegetables consisting of 13 species (19).

The purpose of this study was to evaluate the effects of water deficits on germination and germinated seed growth of tomato. The water sensitive phase of the germination process was examined and the performance of germinated and dry seed was evaluated under simulated drying soil conditions. Two species of tomato, Lycopersicon chilense Dun. and Solanum pennellii Corr. which have drought resistant characteristics, were compared to Lycopersicon esculentum Mill.

In this paper the term germinated seed will refer to a seed with the radicle visibly emerged from the seed coat.

Materials and Methods

Seed Germination and Water Stress

Seed of Lycopersicon esculentum cv. Campbell 1327, Lycopersicon

chilense and Solanum pennellii were used in the following experiments. The germination technique was as follows. Seed were placed in an aerated glass column (39.5 cm in length and 4.5 cm in diameter) and filled with distilled water. A constant temperature water bath contained the columns and maintained a 30°C germination temperature. Water in the columns was changed daily. Seed remained in the columns till the average radicle length was 2-3 mm. This required 52, 40 and 36 hours for L. chilense, L. esculentum and S. pennellii, respectively.

The water stress was maintained in all laboratory experiments with polyethylene glycol (PEG) 6000. The equation derived by Michel and Kaufmann (15) was used to obtain the desired osmotic potential of the solution.

$$\psi s = -(1.18 \times 10^{-2})C - (1.18 \times 10^{-4})C^2 + (2.67 \times 10^{-4})CT + (8.39 \times 10^{-7})C^2T$$

ψs --- osmotic potential
C ---- concentration PEG 6000 g/kg H_2O
T ---- temperature in degrees C

Germination and Germinated Seed Growth vs Water Stress

Twenty dry and germinated seed of each species were transferred to 25 x 60 mm petri dishes fitted with 2 pieces of #2 filter paper. Three ml of PEG 6000 solution was placed in each dish. Water deficits ranged from 0 to -8 bars in 2 bar increments.

The experiment was conducted for 6 days in darkness. Three continuous temperatures were evaluated as separate experiments; 25, 30 and 35°C. Temperature was maintained by a General Electric model 806 incubator.

The percent germination and total seedling length was measured for

the dry seed treatment at the end of the 6 day period. From these data, the maximum percent germination, G 50, G 0 and D grow 50 were calculated. The G 50 and G 0 are the water stresses in bars in which germination was reduced 50 and 100 percent, respectively. The D grow 50 is the water stress in bars in which growth of the seed that germinated was reduced 50 percent. Their values were derived by regression analysis of the raw data.

The root (radicle) and shoot (hypocotyl) length was measured for the germinated seed treatments. The root to shoot length ratio and growth rate was determined. The G grow 50 was calculated in the same manner as stated above.

Water Sensitive Phase of Germination

Two experiments were performed to determine which stage in the germination process is most sensitive to water deficits. Fifty seed of each species were placed in aerated water as described previously. At 0, 6, 12, 18 and 24 hours prior to radicle emergence, seed were transferred to 15 x 100 mm petri dishes. Each petri dish was fitted with 1 piece of #3 filter paper and was moistened with 6 ml of -7.0 bar PEG 6000 solution. From earlier studies this water stress was found to be totally inhibitory to the normal germination process for all three species. The temperature was maintained at 25°C. The percent seed with radicles continuing to elongate 48 hours after transfer to the water stress was determined.

A second experiment consisted of 'priming' the seed. Fifty seed of each species were placed in petri dishes containing -7.0 bar solution of PEG 6000 at 25°C. The seed remained in this solution for 96 hours

and the percent germination was calculated. The seed were then transferred to petri dishes containing water for 24 hours. Once again the percent germination was calculated. The seed were finally transferred back to the -7.0 bar water stress and the percent seed with radicles continuing to elongate was determined.

A completely randomized design was used for all the laboratory experiments described. There were 4 replications per treatment.

Seedling Emergence

A Percival (Percival Co.,Boone, Iowa) walk-in incubator was used to maintain desired environmental conditions for the emergence test. A 12 hour photoperiod with 30°C day and 25°C night was used. Flats (50 cm x 36 cm x 7 cm) containing 2 parts sand: 1 part vermiculite were used for the growing medium. Since seedling emergence was the only parameter measured, light intensity was not measured and nutrients were not added to the growing medium.

Screen cage psychrometers (J.R.D. Merril Co., Logan, Utah) and a HR-33T dew point microvoltmeter (Wescor, Inc., Logan, Utah) were used to determine the soil water potential and temperature. Measurements were recorded at 1.5 and 5.0 cm depths.

Flats were initially watered to field capacity and then allowed to dry over the course of the experiment. Seed treatments were sown 2 (norm) and 5 (stressed) days after watering.

Treatments consisted of sowing fifty dry, dry in gel and germinated seed in gel at a 1.5 cm depth. Laponite 508 (Laporte Inc., Hackensack, NJ) at 15 g/l was used. A Waring blender at low speed was used to disperse the laponite in water and form the viscous gel. The gel extrusion rate was 15 ml/m.

Daily emergence data was taken over a 2-week period. The T50, T10-90 and percent emergence was calculated (21). The T50 is the time in days for 50 percent of the seedlings to emerge. The T10-90 is the time span in days for 10 to 90 percent of the seedlings to emerge. The T10-90 is used as a measure of the uniformity of emergence. A seedling was considered emerged when the cotyledons were fully expanded.

After the initial 2-week emergence period, the flats were rewatered and the percent emergence was again determined. There were 4 replications per treatment. A randomized complete block design with a 3 x 2 factorial arrangement of treatments was used.

Results and Discussion

In preliminary experiments, necrosis of the radicle tissue was observed if the water potential of the media was -10 bars or less. Phytotoxicity has been reported due to use of PEG as an osmoticum (12).

The germination of L. chilense and S. pennellii was normal as determined by standard germination testing. No dormancy mechanisms were observed.

Seed Germination and Water Stress

The maximum percent germination was determined for each species at each temperature at 0 bars. Germination of Lycopersicon genus are more sensitive to elevated temperatures than S. pennellii (Table 1).

The maximum cardinal temperature for tomato germination is about 35°C (13). Varietal differences have been shown to exist in tomato germination at high temperatures (1).

The G 50, G 0 and G grow 50 values are more negative for L. escu-

lentum than L. chilense and S. pennellii at 25°C (Table 1). This indicates that the germination parameters of esculentum were less sensitive to water deficits than the two wild species.

The two wild species of tomato tested both have drought resistant characteristics. S. pennellii is drought tolerant and also salt tolerant (4). The root system of S. pennellii amounts to less than 5% of the proportional weight of L. esculentum and its leaves have a high capacity to absorb and retain atmospheric water (18).

L. chilense is a drought avoider having a very extensive root system (18). From these data (Table 1) it can be concluded that the drought mechanism is not observed during germination or early germinated seed growth. Data on sorghum (Sorghum bicolor L. Moench) has shown different cultivars require different seed moisture contents before germination would occur (14). This may be related to seed size or seed composition, which ultimately would affect the amount of water imbibed.

At 35°C no differences were observed in the germination parameters (Table 1). This occurred because at 35°C germination was very low at 0 bars and at -2 bars germination was completely inhibited. The germinated seed continued growth at 35°C with an imposed water stress (Table 1). Thus it appears once a seed is germinated it can continue growth at suboptimal environmental conditions for normal germination to occur.

The G grow 50 values are more negative than the D grow 50 values for each species at each temperature (Table 1). This supports other research (10) that germination is more sensitive to water stress than is growth of a germinated seed.

The growth rates of the germinated L. esculentum seed were greater than the two wild species (Table 1). This can be attributed to differ-

ences in seed size and vigor. The weight per seed in mg was 0.72, 3.30 and 0.52 for L. chilense, L. esculentum and S. pennellii, respectively.

In general, as the water stress of the media increased there was an increase in seedling root to shoot length ratio (Table 2). It was observed at 30 and 35°C at -8 bars that necrosis occurred on S. pennellii. Earlier work on Vicia faba L. showed a similar response on the root and shoot growth to water stress (6).

The increase in the seedling root to shoot length ratio as water stress increases appears to be a general phenomenon. It has been shown in pea (Pisum sativum L.) that root pressure potential and thus growth was maintained as water deficits develop (8). Root to shoot growth alterations have been observed on maize seedlings experiencing water stress (20). The subject of root to shoot alteration, osmotic and solute regulation will be the topic of another paper by this group (22).

Water Sensitive Phase of Germination

Seed with radicles visibly emerged of each species resulted in 91 to 95% continuing growth when transferred to -7 bars water stress (Fig. 1). Germinating seed transferred 6 hours or more prior to radicle emergence resulted in a dramatic decrease in seed that continued growth (Fig. 1). This data indicates the water sensitive phase of germination occurred just prior to radicle emergence.

It has been shown that leaching of inhibitors from the seed coat can promote germination of certain desert species (23). Soaking the seed in water or leaching the seed was not adequate to allow continued growth in a water stress (Fig. 1).

Seed first 'primed' for 4 days at -7 bars resulted in little or no

germination (Table 3). Those imbibed seed of each species were then able to germinate when exposed to water for a 24 hour period. As stated earlier, L. chilense normally requires a longer period of time to germinate than the other species. Due to this fact, L. chilense received a 36 hour water pulse following priming. This resulted in increased percent germination from 57 to 94.5 (Table 3). Those seed, when transferred back to -7 bars, continued radicle elongation. These results are similar to those reported on calabrese and cress (11).

It has been described, in roots, that the initiation of cell elongation is under different metabolic control than elongation itself (16). This hypothesis has been further used to describe the water sensitive phase of germination (9). This can explain why the water sensitive phase of germination occurs just prior to visible radicle emergence.

Seedling Emergence

The soil water potential during the emergence period did not decrease below -2 bars for the 'norm' condition. The soil water potential gradually decreased to about -20 bars at 1.5 cm depth during the emergence period in the 'stress' condition. However, at the end of the emergence period the water potential was approximately -3 bars at the 5 cm depth.

The gel used to extrude the germinated seed was 98.5% water. A treatment of sowing dry seed in gel was thus evaluated to determine the effect of the additional moisture on emergence parameters.

The percent emergence of the dry sown treatments was less than 50% when sown in the stressed soil (Table 4). Emergence of the germinated seed was unaffected by soil water status (Table 4).

Thus the benefit of sowing germinated seed in a marginally stressed soil is that seedling establishment can occur. Though the top 2-3 cm of soil dries out the germinated seed can continue root growth and thus exploit available soil moisture.

The T50 and T10-90 emergence values were less for the germinated sown seed than the dry sown seed (Table 4). In earlier work it was observed that emergence from germinated seed was earlier and more uniform than dry sown seed (3).

For the germinated treatment, the T50 and T10-90 values are lower in the stress than in the norm condition. This can partially be attributed to the differences in soil temperatures during the emergence periods. Due to evaporation the growing medium temperature was about $4C^{o}$ lower in the norm than the stress.

Rewatering the flats resulted in an increase in the emergence of the dry sown treatments of about 15 and 25% for the norm and stress conditions respectively (Table 4). Sowing the dry seed in gel made no significant contributions to the emergence parameters tested.

It can be concluded that if soil conditions become too extreme the germinated seed will perish. The quiescent seed under the same conditions will not germinate until adequate moisture is available.

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Table 1. The effects of water stress on growth parameters of dry and germinated seed of three tomato species at 25, 30 and 35°C.

25°C Species	Maximum percent germination	-Bars G 50	G 0	D grow 50	G grow 50	Growth rate mm/day
L. chilense	82.5a[z]	2.4a	4.9a	2.6a	4.0a	6.4a
L. esculentum	90.0a	3.7b	6.9b	3.2a	5.9b	11.8b
S. pennellii	90.0a	2.8a	5.2a	2.8a	4.8a	7.4a
30°C Species						
L. chilense	65.0a	1.5a	3.0a	1.4b	4.9a	8.6a
L. esculentum	77.5ab	2.9b	5.5b	2.7a	5.1a	12.4b
S. pennellii	90.0b	2.2ab	4.2a	2.3ab	4.8a	8.6a
35°C Species						
L. chilense	5.0a	0.5a	1.0a	0.5a	6.0a	3.8a
L. esculentum	7.5a	0.7a	1.5a	0.7a	7.9b	6.5b
S. pennellii	47.5b	1.0a	2.0a	1.0a	6.3a	5.7ab

[z]Mean separation within columns within temperatures by LSD (.01).

Table 2. The effects of water stress on the root to shoot length ratio of three tomato species at 25, 30 and 35°C.

	Root to shoot length ratio							
	-bars							
25°C Species	0	2	4	6	8	L[z]	Q[y]	C[x]
L. chilense	0.4	0.9	1.5	3.0	3.5	**	NS	NS
L. esculentum	1.6	2.3	3.1	3.7	4.7	**	NS	NS
S. pennellii	1.2	2.7	5.6	7.3	9.4	**	NS	NS
30°C Species								
L. chilense	0.3	0.5	1.2	3.1	4.7	**	**	NS
L. esculentum	0.6	1.0	1.6	3.0	7.2	**	NS	NS
S. pennellii	0.9	1.4	5.1	7.3	3.5	**	**	**
35°C Species								
L. chilense	0.4	0.4	0.5	0.6	2.1	**	**	NS
L. esculentum	0.6	0.6	0.6	0.9	2.7	**	**	NS
S. pennellii	0.8	0.8	1.9	3.1	2.0	**	**	**

[z]Linear.
[y]Quadratic.
[x]Cubic.
*Significant at 5%.
**Significant at 1%.
NSNot Significant.

Fig. 1. The effect of transferring 3 species of tomato seed to -7 bars water stress at various times prior to radicle emergence on continued seedling growth.

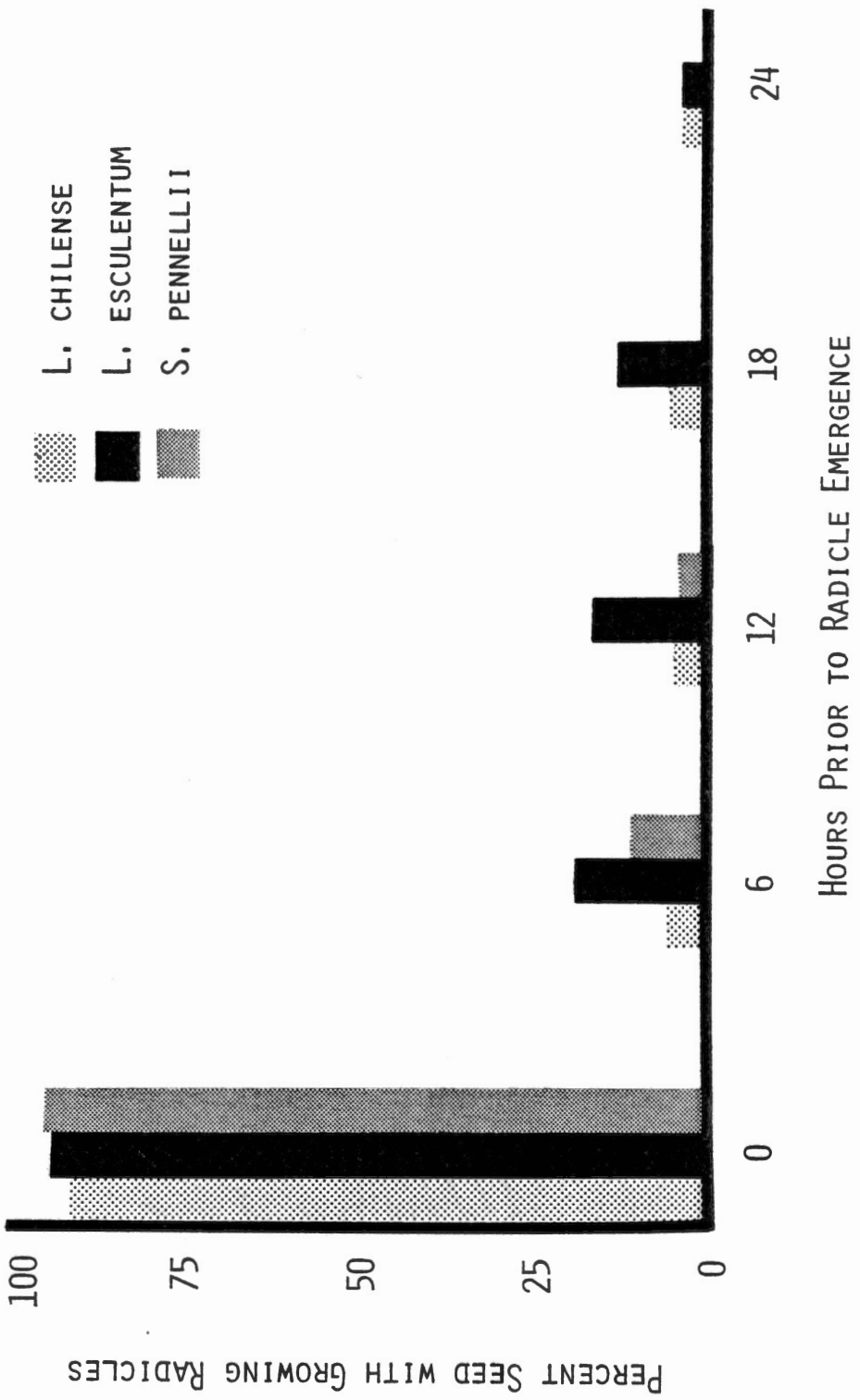
L. CHILENSE
L. ESCULENTUM
S. PENNELLII
PERCENT SEED WITH GROWING RADICLES
100
75
50
25
0
0
6
12
18
24
HOURS PRIOR TO RADICLE EMERGENCE

Table 3. Growth parameters of three tomato species at 25°C after the following sequence; (1) 4 day imbibition at -7 bars, (2) 24 hour water pulse, (3) transfer of seed back to -7 bar solution.

	Percent		
Species	Germination after 4 days at -7 bars	Germination after 24 hour water pulse	Radicles growing after transfer to -7 bars
L. chilense	0.0a[y]	57.0a	59.0a
L. esculentum	5.0a	92.5b	92.0b
S. pennellii	0.0a	95.0b	95.5b
L. chilense[z]	0.0a	94.5b	94.0b

[z]L. chilense received 36 hour water pulse.

[y]Mean separation within columns by LSD (.01).

Table 4. Emergence parameters of dry, dry in gel and germinated tomato cv. Campbell 1327 seed sown in stressed and non-stressed soil.

	Percent emergence		T50 (days)		T10-90 (days)		Percent emergence after rewatering	
Treatment	norm	stress	norm	stress	norm	stress	norm	stress
Dry	76.5	43.0	5.4	5.8	4.9	5.5	90.5	68.0
Dry in gel	79.5	49.0	5.6	5.9	5.2	5.5	89.0	76.0
Germinated in gel	98.5	97.5	3.0	2.7	3.0	2.2	98.5	97.5
LSD (.05) Trt x Stress	14.6		.3		.7		8.5	

CHAPTER V

OSMOTIC AND SOLUTE REGULATION IN GERMINATING TOMATO SEEDLINGS[1]

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Additional Index Words: stress, Lycopersicon esculentum, osmoregulation

Abstract: Seed of tomato Lycopersicon esculentum 'Campbell 1327' were germinated in aerated water and then grown for an additional two days in petri dishes. These germinated seed were then transferred to water stresses of 0 to -6 bars in two bar increments. Mannitol and water was used to obtain the desired water stress of the media. Water relations, growth rates and various solutes were determined for the roots and shoots at different water stresses. As water stress increased osmotic adjustment occurred in the roots which accounted for the maintenance of turgor and growth. During the same period little adjustment occurred in the shoots and consequently growth decreased. Turgor was correlated with growth rates for both plant parts. Reducing sugars, non-reducing sugars,

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amino acids, nitrates, phosphates and potassium generally increased in the roots and decreased in the shoots as water stress increased. Proline increased in both plant parts during the same period. Thus osmotic as well as solute regulation occurred during water deficits. The increase in the root to shoot length ratio appears to be an adaptive feature during periods of water stress.

Introduction

The responses of plants to water deficits has been reviewed (7). Water stress can greatly affect germination and early seedling growth.

Our laboratory has shown that water deficits can affect the root to shoot length ratio (15). Germinated seed of Lycopersicon chilense Dun., Lycopersicon esculentum Mill 'Campbell 1327' and Solanum pennellii Corr. were placed in water stresses of 0 to -8 bars in two bar increments. The known water stresses of the media were obtained with solutions of polyethylene glycol (PEG) 6000 and water. It was observed as the water stress of the media increased, in general, there was an increase in the seedling root to shoot length ratio.

Cell growth is the most sensitive process to water stress. The maintenance of turgor or pressure potential is mandatory for cell growth. Osmoregulation or osmotic adjustment is a process in which turgor is maintained while the water potential decreases. This is accomplished by a decrease in the osmotic potential.

Very young seedlings appear to have a great capacity for osmotic adjustment when water is limiting. Roots of 3 to 5 day old pea (Pisum sativum L.) Seedlings were shown to adjust their osmotic potential when grown in soil ranging in water potential from -2.8 to -8.3 bars. Root

pressure potential was maintained and growth unaffected by decreasing the soil water potential. It was assumed that a net accumulation of solutes occurred, but the solutes were not identified or quantified in the study.

An increase in the root to shoot dry weight ratio has been observed during stress (4). It has been suggested that roots osmotically adjust to a greater extent than the shoots of many species (7).

The purpose of this study is to evaluate the effects of water stress on the growth of roots and shoots of germinated tomato seedlings. Measurements of the water relations and osmotically active solutes of roots and shoots will be used to evaluate osmotic regulation and turgor maintenance.

In this paper the terms root and shoot will be used to describe germinating seed parts rather than radicle and hypocotyl, respectively.

Materials and Methods

Seed Germination and Water Stress

Seed of tomato Lycopersicon esculentum cv. Campbell 1327 was used in all experiments. Seed were placed in an aerated glass column (39.5 cm in length and 4.5 cm in diameter) and filled with distilled water. The glass columns were placed in a constant temperature water bath which maintained a 30°C germination temperature. Water in the columns was changed daily. Seed remained in the column 48 hours till the average radicle length was 3 mm.

After germination, seed were transferred to 150 x 25 mm petri dishes fitted with one piece of #3 filter paper. The filter paper was moistened with 10 ml of deionized distilled water. Germinated seed were grown in darkness for an additional 40 hours. Temperature was maintained at a

constant 30°C by a General Electric Model 806 incubator.

The seedlings were then transferred to known water stresses in petri dishes with filter paper as described. Water deficits were obtained by solutions of mannitol in deionized water. Water stresses ranged from 0 to -6 bars in two bar increments. Ten ml of mannitol solution was placed in each dish. Seedlings were incubated in darkness at 30°C for 24 hours.

Preliminary experiments have shown that osmotic adjustment had occurred after this period of time. Seedlings were prepared in this manner for the following experiments. There were four replications per treatment in all experiments.

Seedling Growth

Ten seedlings were prepared as described. After the 24 hour water stress the root and shoot length of each seedling was measured. Growth continued for an additional 24 hours and then remeasured. The growth rate in mm/day was calculated.

Water Relations

Plant tissue water relations were measured with a HR-33T dew point microvoltmeter (Wescor, Inc., Logan, Utah) with three C-52 and one C-51 sample chambers. Each psychrometer was calibrated with known NaCl solutions at 25°C.

Twenty seedlings were disected into roots and shoots. The distal 8 mm section of the root and proximal 8 mm of the shoot was used for determination of water relations. The seed coat and cotyledons were discarded.

Plant parts were briefly washed in distilled water to remove the

mannitol solution. The tissue was blotted and quickly transferred to the sample chamber. Twenty root and ten shoot segments were used per sample chamber. A standard two hour equilibration time was used.

After the water potential was measured the plant tissue holder was removed, stoppered and plunged in liquid nitrogen for 60 seconds. The tissue holder was allowed to thaw and then returned to the sample chamber for another two hour equilibration. The determination of the osmotic potential was thus obtained. The difference between the osmotic and water potentials was used as an estimate of the pressure potential. The matric potential was assumed to be negligible (16).

Measurement of Osmotically Active Solutes

Fifty seedlings were disected into roots and shoots. Seed coats and cotyledons were discarded. The fresh weight was determined for each plant part. Tissue was lyophilized and the dry weight measured.

The tissue was homogenized with 5 ml of deionized distilled water in a Ten Broeck tissue grinder. The homogenizer was rinsed with an additional 5 ml of water. The homogenate was centrifuged for 5 minutes and the precipitate discarded. The following solutes were quantified in the supernatant; reducing sugars, non-reducing sugars, amino acids, proline, nitrates, phosphates, potassium and the electrical conductivity.

The reducing and non-reducing sugars were determined by the Nelson Test (2). The non-reducing sugars were obtained by first hydrolyzing an aliquot of the extract for 10 minutes at $100^{\circ}C$ with 0.2N H_2SO_4.

The amino acid pool and proline was determined with ninhydrin reagent (17,14). Permutit resin was omitted from the proline assay.

The nitrates were quantified with an Orion specific ion electrode

and Orion 901 Ionalizer. Phosphates were determined spectrophotometrically (6). Potassium was determined with a Perkin Elmer Model 303 Atomic Absorption Spectrophotometer. Electrical conductivity (EC) was determined with a Markson Electromark Analyzer Model 4405.

A completely randomized block design was used. Trend analysis was investigated by partioning the treatment sum of squares into single degrees of freedom.

Results and Discussion

In preliminary experiments, erratic water potential values were obtained using PEG 6000 as an osmoticum. It appeared that some of the PEG solution remained on the seedling root tissue after rinsing. Mannitol solutions were not observed to interfere with water relation measurements or the reducing sugar test. Mannitol was considered the best suited osmoticum for these experiments.

Water Relations

Water potential of both the root and shoot decreased as the water potential of the media decreased (Fig. 1). The shoot osmotic potential decreased slightly as the water stress of the media increased (Fig. 2). There was a 3.4 bar decrease in the root osmotic potential over the range of water stresses evaluated (Fig. 2).

Osmotic adjustment is recognized as an effective means of turgor maintenance in plants subjected to water stress (8). Turgor pressure is necessary for cell elongation and thus growth (7).

A significant positive correlation was observed for the growth rates and pressure potential for both roots and shoots (Fig. 3). When turgor

was fairly high a linear relation existed between ψp and leaf elongation rate in sorghum (Sorghum bicolor L. Moench)(8). This linear relation existed until ψp decreased to a certain threshold potential.

This data indicates that root growth can continue during periods of water stress. This is accomplished by osmotic adjustment and thus maintenance of ψp. Shoot growth under the same conditions results in decreased growth due to lack of osmotic adjustment and subsequently decreased ψp.

In contrast to this data, work in soybean (11) (Glycine max L. Merr.) and sunflower (10) (Helianthus annuus L.) seedlings have shown osmotic regulation to occur in the hypocotyls. However, roots were not examined in either study.

Shoot and root growth of corn (Zea mays L.) has been measured during periods of water stress (12). Leaf extension was arrested as water deficits developed. Root growth during the same period was unaffected. Root pressure potential was maintained by a decrease in ψs. Though solutes were not quantified, the authors suggested that solutes were partitioned to the roots so that turgor and hence growth was maintained.

A decrease in tissue ψs can occur by an increase in the solute concentration per cell. These solutes can originate by internal production or by uptake of solutes from the medium. Since osmotically active solutes were not available in the medium, the former hypothesis was explored.

Earlier work on soybean has shown the cotyledons were the source of solutes for osmotic adjustment (11). Removal of the cotyledons prevented osmotic adjustment.

Solute Measurement

In general, as the water stress of the media increased the solute concentration increased in the roots and decreased in the shoots (Tables 1 and 2).

Proline was the only constituent to increase in both the roots and shoots as water stress increased (Table 1). Proline has been found to increase by more than ten fold in leaves of water stressed barley (Hordeum vulgare L.) It has been shown that proline generally accumulates to higher levels in the shoots than roots of water stressed plants (14).

Carbohydrates (reducing and non-reducing sugars) were the most abundant constituents for osmotic adjustment (Tables 1 and 2). Organic acids, primarily malate and citrate, have been reported to be involved in osmotic adjustment processes (1).

Data on seedling sunflower hypocotyls have shown hexoses (glucose and fructose) and organic potassium salts to be the major osmotic constituents (10). It was determined that osmotic pressures and hence turgor were obtained from 1) translocation of sucrose from the cotyledons and later inversion in the hypocotyls and 2) translocation of potassium from the seed to the hypocotyls.

As water stress of the media increased the total solutes measured increased in the roots and decreased in the shoots (Table 3). Water stress did not affect the sum of the solutes from the roots and shoots (Table 3).

This data suggests that there was translocation of existing solutes in the seedling. Solutes were partitioned from the shoots to the roots during periods of water stress.

The shoot to root fresh weight ratio decreased with increased water stress (Table 3). This would indicate that dehydration and thus cell volume decrease was occurring to a greater extent in the shoots than roots. A decrease in the cell volume would increase the solute concentration. Since there was a decrease in the shoot solute concentration as water stress increased (Table 3), a decrease in cell volume would account for the osmotic potentials measured (Fig. 2).

The shoot to root dry weight ratio was not affected by water stress (Table 3). During the same period the shoot to root solute ratio decreased by two fold (Table 3). Thus both solute and osmotic regulation occurred as water stress increased.

The solutes quantified in this study accounted for approximately 35 and 60 percent of the osmotic potentials measured for roots and shoots, respectively (data not shown). Water stressed cotton leaves (Gossypium hirsutum L.) were found to maintain turgor during periods of water stress (3). Analysis of soluble carbohydrates and malate could not account for the ψ_p. The authors concluded that structural changes may play a role in turgor maintenance.

Water stressed sorghum leaves have shown a decrease in tissue elasticity in response to stress (9). Models have been proposed to evaluate the heterogeneity of water relations in root tissue (13). It appears that anatomical changes and compartmentalization is occurring in the plant tissue. Thus measuring the bulk tissue solutes can not totally account for the tissue osmotic potential.

In conclusion, root growth can continue at the expense of shoot growth during periods of water stress. This can be interpreted as an adaptive feature. Survival of the seedling during water deficits would

necessitate root growth i.e. exploit water rather than increased water use and loss due to shoot growth.

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Fig. 1. The water potential of roots and shoots of tomato 'Campbell 1327' incubated at various water stresses.

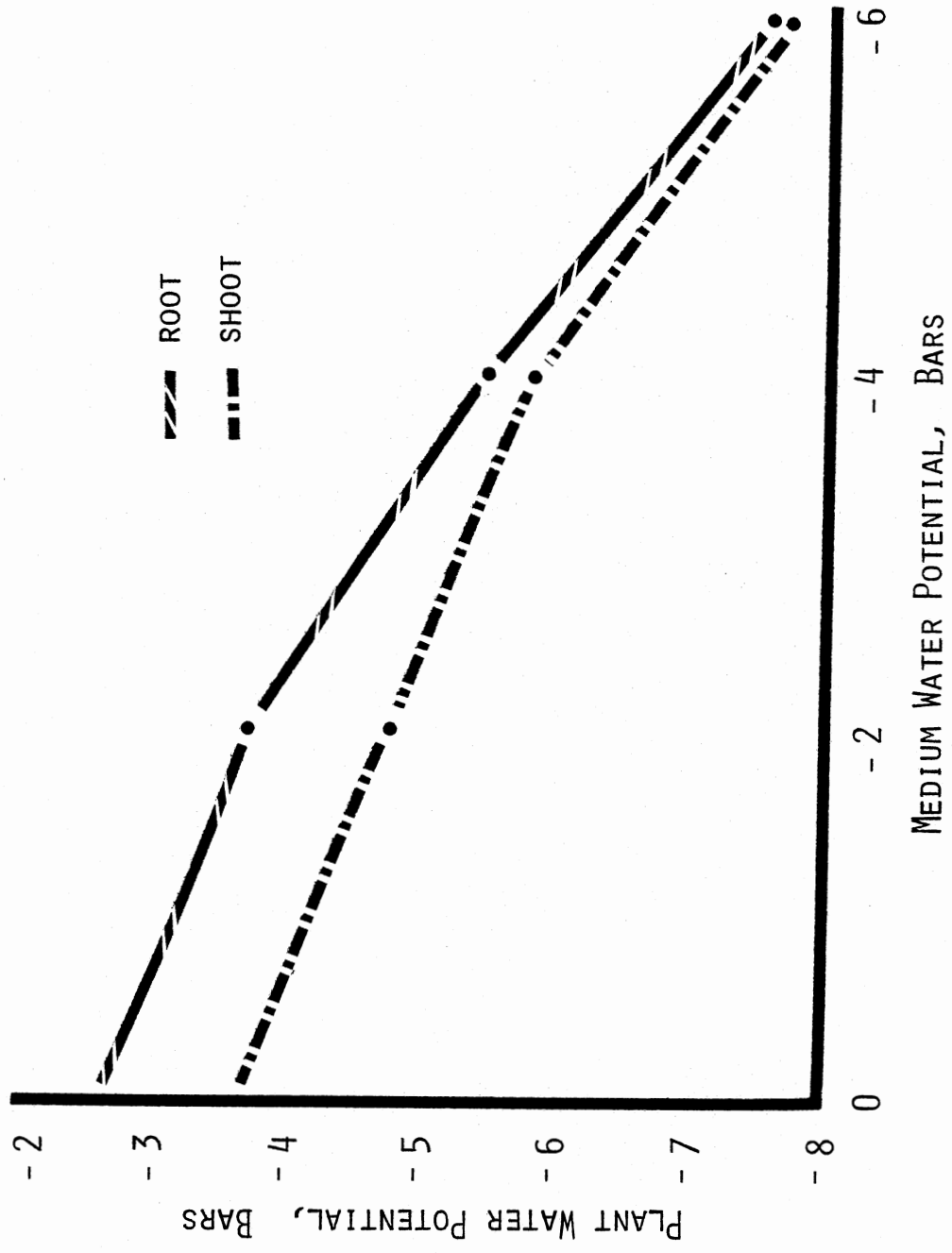
ROOT
SHOOT
-2
-3
-4
-5
-6
-7
-8
PLANT WATER POTENTIAL, BARS
0
-2
-4
-6
MEDIUM WATER POTENTIAL, BARS

Fig. 2. The osmotic potential of roots and shoots of tomato 'Campbell 1327' incubated at various water stresses.

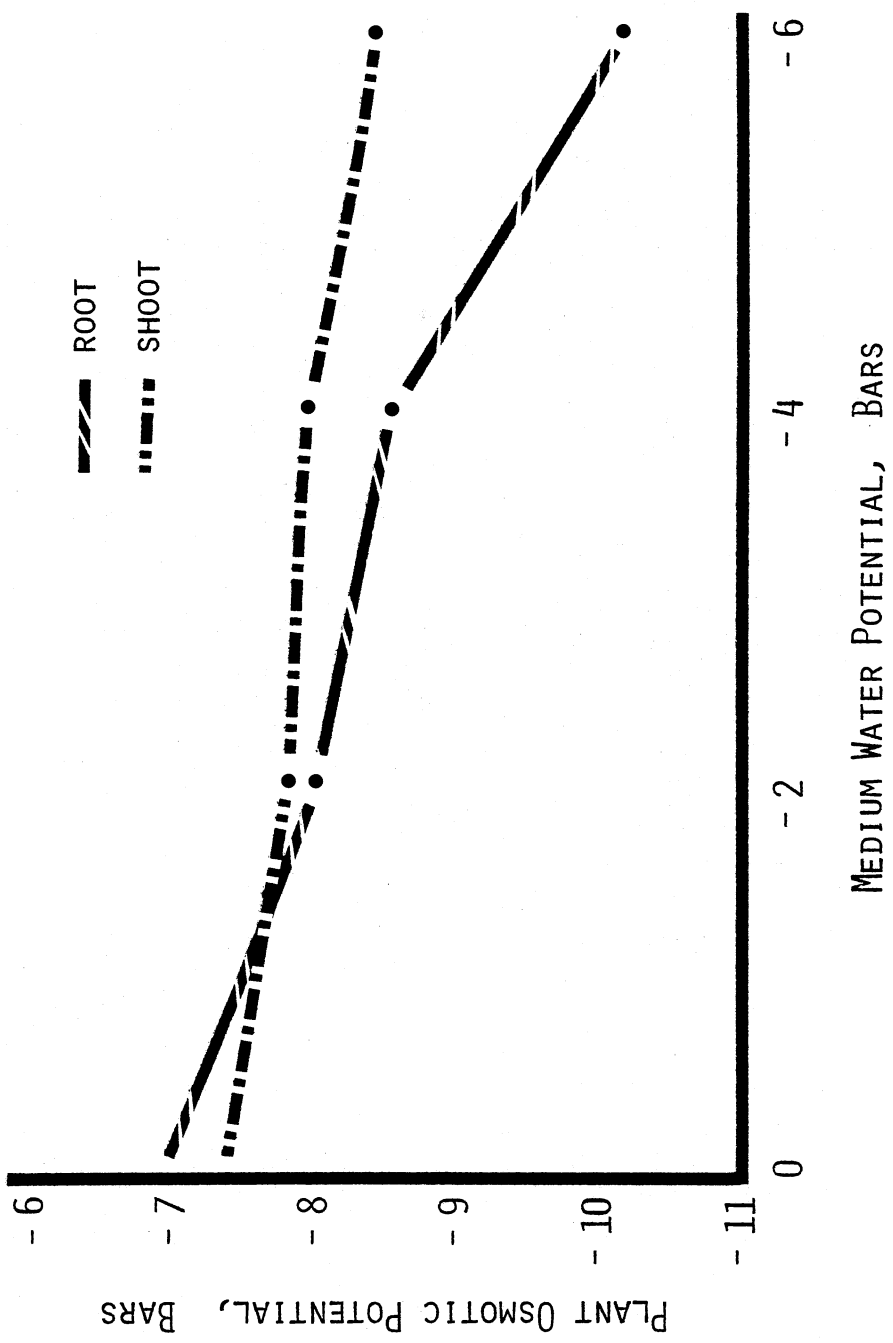
ROOT
SHOOT
-6
-7
-8
-9
-10
-11
0
-2
-4
-6
PLANT OSMOTIC POTENTIAL, BARS
MEDIUM WATER POTENTIAL, BARS

Fig. 3. Regression analysis of growth rate (mm/day) on plant pressure potential (bars) for roots and shoots of tomato 'Campbell 1327'.

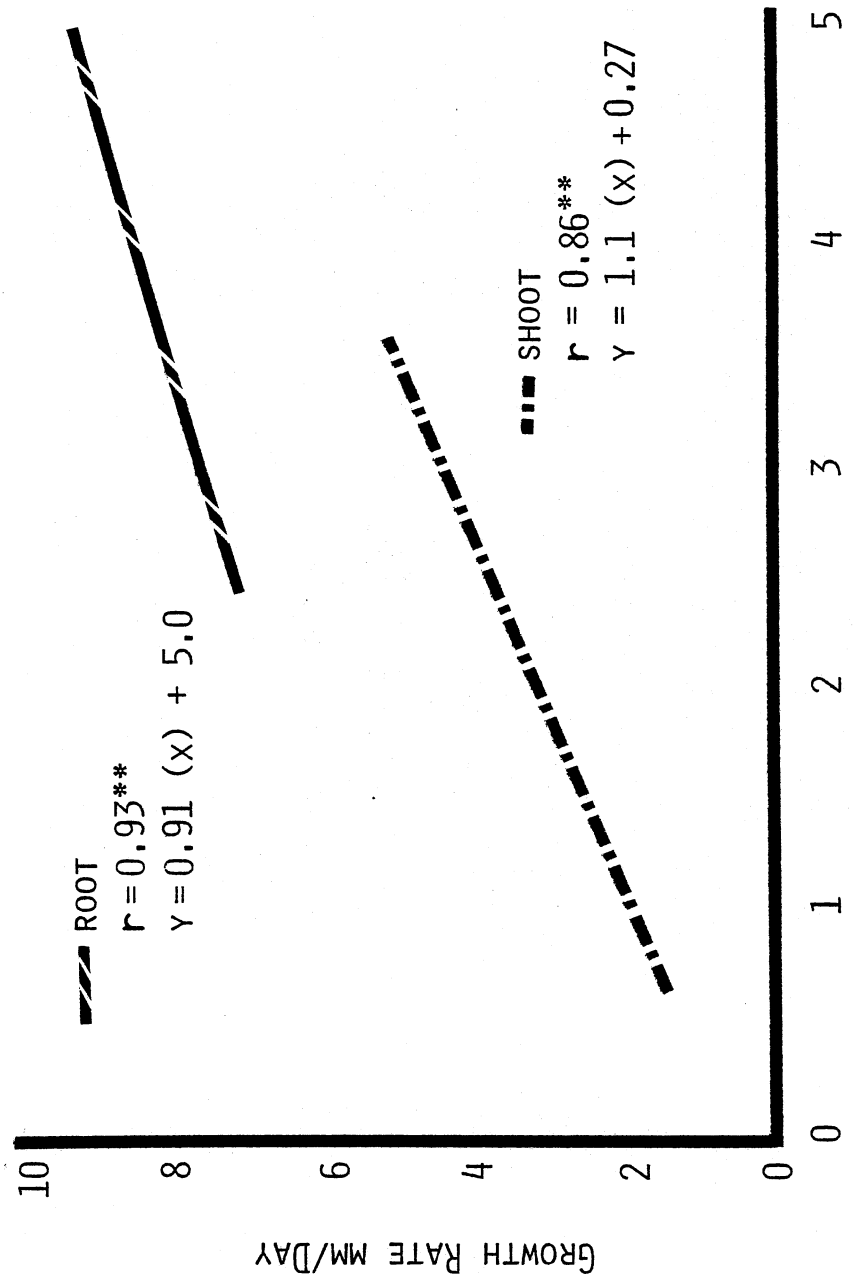
ROOT
r = 0.93**
Y = 0.91 (X) + 5.0
SHOOT
r = 0.86**
Y = 1.1 (X) + 0.27
GROWTH RATE MM/DAY
PLANT PRESSURE POTENTIAL, BARS
0
2
4
6
8
10
0
1
2
3
4
5

Table 1. Quantity of various solutes in roots and shoots of tomato 'Campbell 1327' seedlings at various water stresses.

Stress (-bars)	µg/mg dry weight							
	Reducing sugars		Non-red sugars		Amino acids		Proline	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
0	92	196	51.9	19.4	20.2	86.5	0.4	2.3
2	105	169	57.9	19.7	22.6	54.5	0.8	2.8
4	115	149	63.0	22.8	31.2	44.7	1.7	3.6
6	132	149	68.9	22.2	46.2	40.9	2.0	4.0
Lin	**	**	**	NS	**	**	**	**
Quad	NS	*	NS	NS	NS	NS	NS	NS

* Significant differences at 5%.

**Significant differences at 1%.

NS Not significant.

Table 2. Quantity of various solutes and EC in roots and shoots of tomato 'Campbell 1327' seedlings at various water stresses.

Stress (-bars)	µg/mg dry weight						EC (µmhos/cm) (1 mg dry wt./ml)	
	Nitrate		Phosphate		Potassium			
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
0	6.6	11.0	2.3	2.8	5.5	7.8	122	82.0
2	9.8	5.9	2.6	2.9	6.6	6.3	130	68.6
4	12.0	4.3	2.7	2.6	5.8	5.5	132	65.4
6	15.0	5.4	3.0	2.4	7.5	5.0	126	58.2
Lin	*	*	**	**	**	**	NS	**
Quad	NS	NS	NS	NS	NS	NS	NS	NS

* Significant differences at 5%.

**Significant differences at 1%.

NS Not significant.

Table 3. Quantity of total solutes per plant part for root, shoot and root + shoot and the shoot to root ratio for fresh and dry weight and total solutes of tomato 'Campbell 1327' seedlings at various water stresses.

Stress (-bars)	Total µg solutes/plant part			Shoot to root ratio		
	Root	Shoot	Root + Shoot	Fresh weight	Dry weight	Total solutes
0	28	250	288	3.3	3.6	6.5
2	47	243	290	2.6	4.1	5.1
4	55	220	275	2.4	4.0	4.0
6	66	214	280	2.3	3.8	3.2
Lin	**	*	NS	**	NS	**
Quad	NS	NS	NS	*	NS	NS

* Significant difference at 5%.

* Significant difference at 1%.

NS Not significant.

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APPENDICES

APPENDIX A

SEED SEPARATION STUDIES

TABLE I

SPECIFIC GRAVITY VS. MALTRIN $^{R}250$-WATER AT $10^{o}C$

Specific Gravity	Maltrin/H_2O (grams)	Maltrin/1 H_2O (grams)
1.05	12.6/87.4	143.9
1.06	14.9/85.1	175.5
1.07	17.3/82.7	208.9
1.08	19.6/80.4	244.1
1.09	22.0/78.0	281.6
1.10	24.3/75.7	321.4
1.11	26.7/73.3	363.7
1.12	29.0/71.0	408.6

$y = 234.7(x) + (-233.9)$

x = desired specific gravity

y = grams of Maltrin (weight/weight basis)

NOTE: The solution specific gravity can not be less than 1.00 and its maximum is determined by the saturation point of Maltrin 250 in water.

TABLE II

SPECIFIC GRAVITY VS. SUCROSE-WATER SOLUTION AT 10°C

Specific Gravity	Sucrose/H_2O (grams)	Sucrose/1 H_2O (grams)
1.05	12.1/87.9	137.6
1.06	14.4/85.6	168.2
1.07	16.6/83.4	199.0
1.08	18.9/81.8	233.0
1.09	21.2/78.8	269.0
1.10	23.4/76.6	305.4
1.11	25.7/74.3	345.8
1.12	28.0/72.0	388.8

$y = 226.8(x) + (-226.0)$

x = desired specific gravity

y = grams of sucrose (weight/weight basis)

NOTE: The solution specific gravity can not be less than 1.00 and its maximum is determined by the saturation point of sucrose in water.

TABLE III

SPECIFIC GRAVITY VS. ACETONE-DICHLOROMETHANE
(DCM OR METHYLENE CHLORIDE)

Specific Gravity	Acetone/Dichloromethane (mls)
0.80	98/2
0.85	89/11
0.90	77/23
0.95	70/30
1.00	58/42
1.05	50/50
1.10	40/60
1.15	32/68
1.20	22/78
1.25	13/87
1.30	5/95

$y = 246.6(x) + (-186.9)$

x = desired specific gravity

y = mls of acetone (vol/vol basis)

NOTE: Specific gravity range is from .79-1.33 using these solvents.

TABLE IV

THE IMBIBED SEED DENSITY DISTRIBUTION OF LETTUCE CV. MESA 659 AND PEPPER CV. CALIFORNIA WONDER SELECT

Specific Gravity	Percent of Total
Lettuce	
1.09	15.5
1.08	43.8
1.07	32.7
1.06[z]	4.6
1.05[z]	2.9
1.04[z]	0.4
Pepper	
1.12	16.6
1.11	60.8
1.10	19.0
1.09[z]	2.3
1.08[z]	1.0
1.07[z]	0.3

[z]Seed of this specific gravity were discarded.

TABLE V

THE PERCENT AND RECOVERY OF GERMINATED LETTUCE CV. MESA 659 AND PEPPER CV. CALIFORNIA WONDER SELECT SEED AFTER POST-RADICLE EMERGENCE SEPARATION

	Percent (± SE)	
Density Fraction	Germinated Seed After Separation	Recovery of Germinated Seed
Lettuce		
Heavy (1.08)	95.8	99.1
Medium (1.07)	98.3	99.3
Light (1.06)	97.3	98.8
TOTAL	97.6 ± .13	99.1 ± .10
Pepper		
Heavy (1.12)	98.0	97.1
Medium (1.11)	98.1	98.5
Light (1.10)	98.5	99.5
TOTAL	98.1 ± .06	98.5 ± .08

Percent germination without separation, 86.3 ± .39 and 80.6 ± .47 for lettuce and pepper, respectively.

TABLE VI

THE PERCENT AND RECOVERY OF GERMINATED LETTUCE CV. MESA 659 AND PEPPER CV. CALIFORNIA WONDER SELECT SEED AFTER A ONCE-OVER SEPARATION

Separation Density	Percent (± SE) Germinated Seed After Separation	Recovery of Germinated Seed
Lettuce		
1.08	92.8 ± .35	100.0 ± 0.00
1.07	95.4 ± .24	95.0 ± 1.12
1.06	96.2 ± .06	81.3 ± 0.80
Pepper		
1.12	83.9 ± .27	100.0 ± 0.00
1.11	96.1 ± .62	96.8 ± 0.02
1.10	97.0 ± .04	85.4 ± 0.83

Percent germination without separation, 86.3 ± .39 and 80.6 ± .47 for lettuce and pepper, respectively.

APPENDIX B

WATER STRESS STUDIES

TABLE VII

THE EFFECTS OF WATER STRESS ON THE PERCENT GERMINATION OF THREE TOMATO SPECIES AT 25, 30, AND 35°C

25°C	Percent Germination							
	medium water potential, -bars							
Species	0	2	4	6	8	L	Q	C
L. chilense	82.5	45.0	10.0	0.0	0.0	**	**	NS
L. esculentum	90.0	87.5	35.0	5.0	0.0	**	**	NS
S. pennellii	90.0	75.0	10.0	0.0	0.0	**	**	NS
30°C								
Species								
L. chilense	65.0	12.5	0.0	0.0	0.0	**	**	NS
L. esculentum	77.5	62.5	12.5	0.0	0.0	**	**	NS
S. pennellii	90.0	60.0	0.0	0.0	0.0	**	**	NS
35°C								
Species								
L. chilense	5.0	0.0	0.0	0.0	0.0	*	NS	NS
L. esculentum	7.5	0.0	0.0	0.0	0.0	**	NS	NS
S. pennellii	47.5	0.0	0.0	0.0	0.0	**	**	NS

* Significant differences at 5 %.

**Significant differences at 1 %.

NS-Not significant.

TABLE VIII

THE EFFECTS OF WATER STRESS ON TOTAL DRY SEEDLING GROWTH OF THREE TOMATO SPECIES AT 25, 30, AND 35°C

25°C	Total Seedling Growth (mm)							
	medium water potential, -bars							
Species	0	2	4	6	8	L	Q	C
L. chilense	42.0	29.8	6.4	0.0	0.0	**	**	NS
L. esculentum	64.5	51.0	12.9	3.0	0.0	**	**	NS
S. pennellii	50.9	46.9	14.7	0.0	0.0	**	**	NS
30°C								
Species								
L. chilense	50.0	9.1	0.0	0.0	0.0	**	**	NS
L. esculentum	59.0	42.0	8.6	0.0	0.0	**	**	NS
S. pennellii	50.4	37.6	0.0	0.0	0.0	**	**	NS
35°C								
L. chilense	7.5	0.0	0.0	0.0	0.0	**	NS	NS
L. esculentum	14.0	0.0	0.0	0.0	0.0	**	*	NS
S. pennellii	19.2	0.0	0.0	0.0	0.0	**	*	NS

* Significant differences at 5%.

**Significant differences at 1%.

NS-Not significant.

TABLE IX

THE EFFECTS OF WATER STRESS ON ROOT GROWTH OF THREE TOMATO SPECIES AT 25, 30, AND 35°C

25°C	Root Growth (mm) medium water potential, -bars							
Species	0	2	4	6	8	L	Q	C
L. chilense	11.4	10.9	9.0	8.5	5.6	**	NS	NS
L. esculentum	38.8	42.1	38.1	26.7	16.0	**	**	NS
S. pennellii	23.9	20.9	22.6	17.1	5.1	**	**	NS
30°C								
Species								
L. chilense	11.6	12.2	16.8	15.0	8.6	NS	**	NS
L. esculentum	26.7	30.7	27.3	25.1	22.9	NS	NS	NS
S. pennellii	24.2	23.7	27.8	17.0	3.1	**	**	NS
35°C								
Species								
L. chilense	6.5	5.8	5.9	5.4	2.3	**	*	NS
L. esculentum	15.1	11.1	10.1	11.4	10.5	**	*	NS
S. pennellii	15.4	13.4	18.3	13.6	5.8	*	*	NS

* Significant differences at 5%.

**Significant differences at 1%.

NS-Not significant.

TABLE X

THE EFFECTS OF WATER STRESS ON SHOOT GROWTH OF THREE TOMATO SPECIES AT 25, 30, AND 35°C

25°C	Shoot Length (mm)							
	medium water potential, -bars							
Species	0	2	4	6	8	L	Q	C
L. chilense	26.9	12.2	6.3	2.9	1.8	**	**	NS
L. esculentum	31.7	22.7	12.6	7.7	3.4	**	NS	NS
S. pennellii	20.2	8.0	4.2	2.4	0.7	**	**	NS
30°C								
Species								
L. chilense	39.7	22.3	14.4	5.0	1.8	**	**	NS
L. esculentum	47.5	32.0	17.1	8.6	2.8	**	**	NS
S. pennellii	27.5	16.6	7.2	2.3	0.9	**	**	NS
35°C								
Species								
L. chilense	16.4	13.8	12.4	8.4	1.1	**	*	NS
L. esculentum	23.7	19.8	17.9	14.4	5.4	**	*	NS
S. pennellii	18.9	18.0	9.9	4.5	2.8	**	NS	NS

* Significant differences at 5%.

**Significant differences at 1%.

NS-Not significant.

TABLE XI

THE EFFECTS OF WATER STRESS ON THE GROWTH RATE OF THREE TOMATO SPECIES AT 25, 30, AND 35°C

25°C	Growth Rate (mm/day) medium water potential, -bars							
Species	0	2	4	6	8	L	Q	C
L. chilense	6.4	3.9	2.6	1.9	1.2	**	**	NS
L. esculentum	11.8	10.8	8.4	5.7	3.2	**	NS	NS
S. pennellii	7.4	4.8	4.4	3.3	0.9	**	NS	NS
30°C								
Species								
L. chilense	8.6	5.8	5.2	3.3	1.7	**	NS	NS
L. esculentum	12.4	10.5	7.4	5.5	4.3	**	NS	NS
S. pennellii	8.6	6.7	5.8	3.2	0.7	**	NS	NS
35°C								
Species								
L. chilense	3.8	3.3	3.0	2.3	0.6	**	**	NS
L. esculentum	6.5	5.2	4.7	4.3	2.7	**	NS	*
S. pennellii	5.7	5.2	4.7	3.0	1.4	**	NS	NS

* Significant differences at 5%.

**Significant differences at 1%.

NS-Not significant.

TABLE XII

THE EFFECTS OF WATER STRESS ON TOTAL GERMINATED SEEDLING GROWTH OF THREE TOMATO SPECIES AT 25, 30, AND 35°C

25°C	Total Seedling Growth (mm)							
	medium water potential, -bars							
Species	0	2	4	6	8	L	Q	C
L. chilense	38.3	23.2	15.3	11.4	7.4	**	NS	NS
L. esculentum	70.6	64.8	50.7	34.4	19.3	**	NS	NS
S. pennellii	44.1	28.9	26.5	19.6	5.8	**	NS	NS
30°C								
Species								
L. chilense	51.4	34.6	31.2	20.0	10.4	**	NS	NS
L. esculentum	74.2	62.7	44.4	33.2	25.7	**	NS	NS
S. pennellii	51.7	40.3	35.0	19.3	4.0	**	NS	NS
35°C								
Species								
L. chilense	22.8	19.8	18.3	13.8	3.4	**	**	NS
L. esculentum	38.8	30.9	27.9	25.8	15.9	**	NS	*
S. pennellii	34.3	31.4	28.2	18.1	8.5	**	NS	NS

* Significant differences at 5%.

**Significant differences at 1%.

NS-Not significant.

TABLE XIII

THE EFFECT OF TRANSFERRING GERMINATING SEED OF THREE TOMATO SPECIES TO -7.0 BAR WATER STRESS AT VARIOUS TIMES PRIOR TO RADICLE EMERGENCE ON CONTINUED SEEDLING GROWTH

	Percent Seed Continuing Growth After Transfer To Water Stress (hours prior to radicle emergence)				
Species	0	6	12	18	24
L. chilense	91.0	5.0	3.0	4.0	2.0
L. esculentum	94.0	21.0	15.0	12.0	2.0
S. pennellii	95.0	11.0	2.0	0.0	0.0

TABLE XIV

THE PERCENT CUMULATIVE DAILY EMERGENCE, TOTAL PERCENT EMERGENCE AFTER REWATERING, MDE AND EV FOR DRY, DRY PLUS GEL AND GERMINATED TOMATO SEED SOWN IN NORMAL AND STRESSED SOIL

		Percent Cumulative Emergence (days)									
Condition	Treatment	3	4	5	6	7	8	9	%EAW[z]	MDE[y]	EV[x]
Normal	Dry	0	0	17.5	61.0	72.5	76.5	76.5	90.5	9.3	98.2
	Dry + Gel	0	0	8.5	55.0	74.0	77.5	79.5	89.0	9.4	99.4
	Germinated	63.0	96.5	97.5	98.5	98.5	98.5	98.5	98.5	18.7	452.8
Stressed	Dry	0	.5	8.0	26.0	35.0	40.0	43.0	68.0	5.0	27.8
	Dry + Gel	0	1.0	6.5	37.5	42.0	46.5	49.0	76.0	5.4	38.8
	Germinated	69.5	95.5	97.5	97.5	97.5	97.5	97.5	97.5	22.0	550.5

%EAW[z] = Percent emergence after rewatering

MDE[y] = Mean daily emergence

EV[x] = Emergence value

TABLE XV

THE MEASUREMENT OF WATER RELATIONS AND GROWTH RATES OF SHOOTS AND ROOTS OF TOMATO SEEDLINGS

Stress (-bars)	-bars				bars			
	Water Potential		Osmotic Potential		Pressure Potential		Growth Rate mm/Day	
	root	shoot	root	shoot	root	shoot	root	shoot
0	2.7	3.6	6.9	7.3	4.2	3.7	9.0	5.0
2	4.3	4.8	8.0	7.8	3.7	3.0	8.2	3.3
4	5.6	5.9	8.5	7.7	3.0	1.9	7.9	1.5
6	7.7	7.7	10.3	8.3	2.6	0.6	7.3	0.8
Linear	**	**	**	NS	**	**	**	**
Quadratic	NS	NS	NS	NS	NS	NS	NS	NS

TABLE XVI

THE µg OF VARIOUS SOLUTES PER PLANT PART FOR ROOTS AND SHOOTS OF TOMATO SEEDLINGS OF VARIOUS WATER STRESSES

	µg/Plant Part							
Stress	Reducing Sugars		Non-red. Sugars		Amino Acids		Proline	
(-bars)	root	shoot	root	shoot	root	shoot	root	shoot
0	19.6	151	11.1	11.1	4.33	65.8	0.09	1.80
2	24.2	158	13.4	18.3	5.15	50.9	0.18	2.64
4	27.4	141	14.9	21.7	7.43	42.2	0.40	3.38
6	31.9	139	16.6	20.7	11.1	38.2	0.46	4.05
Linear	**	NS	**	NS	**	**	**	**
Quadratic	NS	NS	NS	NS	*	NS	NS	NS

TABLE XVII

THE μg OF VARIOUS SOLUTES PER PLANT PART FOR ROOTS AND SHOOTS OF TOMATO SEEDLINGS AT VARIOUS WATER STRESSES

	μg/Plant Part							
Stress	Nitrates		Phosphates		Potassium		Total	
(-bars)	root	shoot	root	shoot	root	shoot	root	shoot
0	1.44	8.64	0.50	2.14	1.17	5.97	38.4	250
2	2.30	5.38	0.60	2.72	1.51	5.85	47.3	243
4	2.89	4.10	0.64	2.50	1.62	5.18	55.2	220
6	3.65	5.04	0.72	2.25	1.81	4.65	66.3	214
Linear	NS	NS	**	NS	**	**	**	**
Quadratic	NS	NS	NS	**	NS	NS	NS	NS

TABLE XVIII

THE CALCULATED OSMOTIC POTENTIAL OF VARIOUS SOLUTES FOR ROOTS AND SHOOTS OF TOMATO SEEDLINGS AT VARIOUS WATER STRESSES

Stress	-bars (Calculated)							
	Reducing Sugars		Non-red. Sugars		Amino Acids		Proline	
(-bars)	root	shoot	root	shoot	root	shoot	root	shoot
0	0.781	1.82	0.233	0.095	0.309	1.43	0.006	0.034
2	0.963	2.45	0.281	0.150	0.369	1.41	0.011	0.064
4	1.12	2.40	0.326	0.196	0.543	1.29	0.026	0.090
6	1.46	2.82	0.402	0.221	0.917	1.39	0.033	0.127
Linear	**	**	**	**	**	NS	**	**
Quadratic	NS	NS	NS	NS	*	NS	NS	NS

TABLE XIX

THE CALCULATED OSMOTIC POTENTIALS OF VARIOUS SOLUTES FOR ROOTS AND SHOOTS OF TOMATO SEEDLINGS AT VARIOUS WATER STRESSES

	-bars (Calculated)							
Stress	Nitrate		Phosphates		Potassium		Total	
(-bars)	root	shoot	root	shoot	root	shoot	root	shoot
0	0.165	0.301	0.038	0.048	0.214	0.331	1.75	4.06
2	0.261	0.241	0.045	0.079	0.278	0.418	2.21	4.81
4	0.349	0.202	0.050	0.080	0.301	0.407	2.72	4.67
6	0.478	0.298	0.062	0.086	0.382	0.436	3.73	5.37
Linear	NS	NS	**	**	**	**	ND	
Quadratic	NS	NS	NS	**	NS	*		

ND-Not determined

TABLE XX

THE FRESH TO DRY WEIGHT RATIO AND RESPIRATION RATES OF ROOTS AND SHOOTS OF TOMATO SEEDLINGS AT VARIOUS WATER STRESSES

Stress	Fresh wt./ Dry wt.		Respiration Rate			
			ul O_2/g fr wt/min		ul O_2/g dry wt/min	
(-bars)	root	shoot	root	shoot	root	shoot
0	24.7	24.3	7.02	2.71	135	69.6
2	17.8	18.7	6.19	2.52	109	47.4
4	14.9	15.9	7.13	3.11	106	49.6
6	14.1	15.5	8.43	3.58	120	55.5
Linear	*	**	*	**	NS	*
Quadratic	NS	**	*	*	*	**

TABLE XXI

THE GROWTH OF ROOT, SHOOT AND TOTAL LENGTH OF GERMINATED TOMATO SEED TREATED WITH VARIOUS SOLUTES

Plant Part	Stress (-bars)	Control	KNO_3	KCl	Sucrose
Root	0	33.7	29.8	32.7	42.9
	2	34.7	27.6	30.8	42.2
	4	30.3	22.3	26.9	34.6
	6	23.4	18.8	21.4	28.7
Shoot	0	27.9	33.1	42.9	27.9
	2	23.0	29.0	26.6	23.0
	4	17.4	21.5	20.5	17.1
	6	12.6	14.6	14.2	12.0
Total	0	61.6	63.0	64.4	70.7
	2	57.8	56.6	57.4	65.2
	4	47.7	43.9	47.4	51.7
	6	36.0	33.4	35.5	40.7

[z]Seed were treated for 6 hours at time of radicle emergence with 20 mM sucrose. Each treatment included 0.5 mM $CaSO_4$. Germinated seed were then transferred to different water stresses and growth parameters were measured after 48 hours.

TABLE XXII

THE ROOT TO SHOOT RATIO AND PERCENT PROMOTION OF ROOT AND SHOOT GROWTH OF GERMINATED TOMATO SEED TREATED[z] WITH VARIOUS SOLUTES

Stress (-bars)	Root to Shoot Ratio			
	Control	KNO_3	KCl	Sucrose
0	1.21	.91	1.17	1.54
2	1.51	.95	1.33	1.83
4	1.73	1.05	1.55	2.03
6	1.86	1.30	1.71	2.39

	Percent Promotion of Growth					
	KNO_3		KCl		Sucrose	
	root	shoot	root	shoot	root	shoot
0	-2.2	13.8	-10.2	18.7	27.6	-0.1
2	-10.9	15.8	-19.5	26.0	22.3	-0.1
4	-8.8	18.1	-24.9	24.0	17.4	-1.4
6	-8.0	13.4	-19.3	16.3	22.9	-4.1

[z]Seed were treated for 6 hours at time of radicle emergence with 20 mM sucrose. Each treatment included 0.5 mM $CaSO_4$. Germinated seed were then transferred to different water stresses and growth parameters were measured after 48 hours.

TABLE XXIII

EMERGENCE PARAMETERS OF GERMINATED TOMATO SEED TREATED[z] WITH VARIOUS SOLUTES SOWN IN WATER STRESSED AND NONSTRESSED SOIL

	Percent Emergence		EV[y]		T50		T10-90	
Treatment	Norm	Stress	Norm	Stress	Norm	Stress	Norm	Stress
Control	98.0	47.0	651	116	3.1	3.3	3.5	3.5
KCl	97.0	47.0	504	174	3.2	3.2	3.5	3.3
KNO_3	96.0	36.0	504	79	3.1	3.4	3.5	3.4
Sucrose	89.0	22.0	368	34	3.3	3.5	3.5	3.2
LSD(.05)								
Trt.	NS		130.5		.15		NS	
Stress	11.0		92.3		.10		NS	
T x S	NS		NS		NS		NS	

[z]Seed were treated for 6 hours at time of radicle emergence with 20 mM KCl, 20 mM KNO_3 or 40 mM sucrose. Each treatment included 0.5 mM $CaSO_4$. Seed of each treatment were sown in flats with 2:1 sand:vermiculite with 12 hour photoperiod 30°C day and 25°C night.

[y]Emergence value.

APPENDIX C

OXYGEN STRESS STUDY

TABLE XXIV

GROWTH PARAMETERS OF DRY AND GERMINATED TOMATO SEED AT VARIOUS OXYGEN LEVELS[z] AFTER 7 DAYS AT 30°C

Treatment	Parameter	Percent Oxygen									Germ 50	Germ 0	Germ 50
		21	10	5	2	1	0.5	L	Q	C			
Dry	Percent Germination	87.0	75.0	52.0	3.0	0.0	0.0	**	**	NS	4.5	1.3	---
	Growth (mm)	92	86	63	1	0.0	0.0	**	**	NS	---	---	4.1
Germinated	Growth Rate (mm/day)	19.9	22.7	23.3	18.2	10.3	7.4	**	**	NS	---	---	1.2
	Root/Shoot	0.85	0.91	0.94	0.84	0.73	0.76	NS	NS	NS	---	---	---

[z]Gas composition was maintained in sealed quart jars containing activated charcoal and $KMnO_4$. The remainder of the gas was nitrogen.

VITA 2

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Doctor of Philosophy

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